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Species shifts in above-ground vegetation and the soil seed bank in the inter-dune lowlands of an active dune field in Inner Mongolia, China

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Abstract

Degradation of semi-arid ecosystems leading to desertification presents a global environmental challenge. However, few studies have investigated seed bank and above-ground species composition in degraded semi-arid dune systems, particularly in relation to their potential to contribute to stabilisation and revegetation. We determined whether soil seed bank and above-ground species composition differed along a chronosequence in the inter-dune lowlands of an active dune field in Inner Mongolia, China. Soil cores were collected in early April 2011 and soil seed bank composition determined using a combination of the seedling emergence and seed extraction methods. Established vegetation, including species composition and abundance, was also surveyed. Relative importance values for all above-ground species and similarities in species composition of vegetation and soil seed bank along the chronosequence were analysed. A clear successional trend was shown for established vegetation along the first three stages identified, followed by a final stage reverting to more mobile substrate due to disturbance by dune movement. This trend was not reflected in the seed bank. Plant and seed bank density increased over time, however, species composition of the seed bank reflected earlier stages rather than the corresponding established vegetation. There was a relationship between established vegetation and the soil seed bank at the earliest stage, driven mainly by the persistence of seeds of the pioneer species *Agriophyllum squarrosum* and *Corispermum candelabrum*. A relatively close relationship was also found at the final stage, where frequent disturbance occurred as a result of increasing sand burial, caused by constant directional sand dune movement. While a clear relationship between the seed bank and associated vegetation was not found along the whole chronosequence,

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the seed bank displayed potential for restoration of pioneer psammophytes and annual herb species, suggesting that it would contribute to regeneration, as well as support latter-stage annuals and several rare and endemic species.

Zusammenfassung

Die Degradation von semi-ariden Ökosystemen, die zur Desertifikation führt, stellt eine globale Umweltherausforderung dar. Indessen haben nur wenige Studien die Samenbank und die oberirdische Artenzusammensetzung in degradierten semi-ariden Dünensystemen untersucht, insbesondere in Hinblick auf die Stabilisierung und Wiederbegrünung. Wir bestimmten, ob die Samenbank im Boden und die oberirdische Artenzusammensetzung entlang einer zeitlichen Entwicklungsreihe in den Dünentälern eines aktiven Dünenfeldes in der Inneren Mongolei (China) differierten. Bodenproben wurden früh im April 2011 gesammelt, und die Samenbank wurde mit einer Kombination aus Keimungsversuchen und Samenextraktion bestimmt. Die vorhandene Vegetation, einschließlich der Artenzusammensetzung und Abundanz, wurde ebenfalls registriert. Die ‘importance values’ (IV) der oberirdischen Arten und die Ähnlichkeiten in der Artenzusammensetzung von Vegetation und Samenbank wurden entlang der Entwicklungsreihe analysiert. Ein eindeutiger Sukzessionstrend wurde für die Vegetation der ersten drei Stadien identifiziert, gefolgt von einem Endstadium, das zu einem mobileren Substrat infolge der Störung durch die Dünenbewegung zurückkehrte. Dieser Trend zeigte sich nicht in der Samenbank. Die Pflanzendichte und die Samenbank nahmen im Laufe der Zeit zu. Allerdings entsprach die Artenzusammensetzung der Samenbank eher früheren Sukzessionsstadien als der aktuellen Vegetation. Es gab eine Beziehung zwischen der vorhandenen Vegetation und der Samenbank im ersten Sukzessionsstadium, die hauptsächlich durch die Persistenz der Pionierarten *Agriophyllum squarrosum* und *Corispermum candelabrum* bestimmt war. Eine relative enge Beziehung wurde auch im Endstadium gefunden, in dem häufige Störungen auftraten, weil zunehmend Pflanzen durch die gerichtete Bewegung der Sanddüne verschüttet wurden. Während eine klare Beziehung zwischen Samenbank und der assoziierten Vegetation nicht über die gesamte zeitliche Entwicklungsreihe gefunden wurde, zeigte die Samenbank das Potential für eine Restaurierung von Pionier-Psammophyten und krautigen Annuellen, was nahelegt, dass die Samenbank zur Regeneration beitragen sowie Anuelle späterer Sukzessionsstadien und seltene und endemische Arten unterstützen könnte.

Keywords: DCA; Chronosequence; Soil seed bank; Inter-dune lowland; Floristic composition; Restoration

Introduction

The soil seed bank is an important component of ecosystem resilience and represents a stock of regeneration potential in many plant assemblages (Hagen, Geelen, & de Vries, 2008). It is especially important for the regeneration of vegetation in habitats where disturbance is frequent (Fenner & Thompson, 2005), such as mobile dunes. Seeds are able to disperse into, accumulate and subsequently germinate in areas devoid of vegetation, such as those found where dunes are forming, to begin the formation of a vegetation layer that will stabilize the sand and form a dune (Leicht-Young, Pavlovic, Grundel, & Frohnapple, 2009). Some species overcome periods of unfavourable weather conditions by building up a large seed bank. For species with this strategy, species diversity is preserved and information on seed bank strategy and structure is retained (Yassir, van der Kamp, & Buurman, 2010). Pioneer species establishment is the initiation of community succession, and soil seed banks can be used to predict the composition of new plant recruitment (Allen & Nowak, 2008).

Inter-dune lowlands are topographic depressions which develop between active dunes, and occur as small, naturally fragmented systems in the dune landscape (Bossuyt, Honnay, & Hermy, 2003; Liu, Li, Yan, & Wu, 2007). In semi-arid dune ecosystems, such as in Inner Mongolia, this landscape consists of a mosaic of mobile dunes, semi-fixed and fixed dunes, and lowland meadows, with a single predominant wind direction (Zhang, Zhao, Zhang, Zhao, & Drake, 2005). The environment contrasts with that on the adjacent active dunes, and fluctuates throughout the year, maintaining standing water in the winter, but prone to drought stress in summer (Stark, Lundholm, & Larson, 2003). Specialised dune plant species are able to withstand mobile sand, burial, drought, high temperatures, salt winds, and low substrate nutrient levels (Gunster, 1994; Pake & Venable, 1996; Stark et al., 2003; Sykes & Wilson, 1987). Subsequently, inter-dune lowlands provide refuge for a relatively large number of rare and endangered species (Gunster, 1994), and are a crucial habitat for the reproduction and survival of invertebrates, amphibians, and other wildlife (Everard, Jones, & Watts, 2010; McLachlan, Kerley, & Rickard, 1996; Peralta-Pelaez & Moreno-Casasola, 2009). It is therefore important to understand the structure and function of inter-dune lowlands, especially to examine vegetation patterns at the dune scale and its relationship with environmental factors in the restoration processes of mobile dunes (Liu et al., 2007). This will improve predictions regarding this resource in the future and guide management decisions for conservation or restoration measures (McLachlan et al., 1996).

Long-term records of vegetation composition almost always show distinct fluctuations in early succession stages followed by a directional change in the later stages (Gunster, 1994; Pegman & Rapson, 2005). Over time, stabilisation and the accumulation of organic material provide an increase in available nutrients and stimulates the growth of strong competitors, as well as shrubs and tree species (Gunster, 1994). In many dune habitats, shrub species occupy older surfaces due to greater substrate stability, decreased sand movement and, in coastal regions, decreased salt spray levels (Pake & Venable, 1996). Semi-arid active dune systems, such as those that occur in China, differ from their coastal counterparts because older surfaces are found in the inter-dune lowlands, adjacent to the leeward slopes of mobile dunes (Liu et al., 2007; Yan et al., 2005; Zhang et al., 2005). Continued deposition of sand from the leeward slope ensures that some of the oldest sections consist of a mixture of wetter lowlands and drier sand (Liu et al., 2007).

Vegetation and their associated soil seed banks have been investigated in dune systems around the world, primarily focusing on coastal dunes (Bossuyt, Stichelmans, & Hoffmann, 2005b; Monserrat, Celsi, & Fontana, 2012; Peralta-Pelaez & Moreno-Casasola, 2009; Plassmann, Jones, & Edwards-Jones, 2010; Smith, Hanley, & Killingbeck, 2008). Very few studies have been conducted in semi-arid mobile dune systems (Liu et al., 2007; Zuo et al., 2008) or looked at the relationship between the soil seed bank and above-ground vegetation along a chronosequence (but see Yan et al., 2005). The differences in development of these semi-arid mobile systems compared with coastal dunes highlights the need for such a study, in order to gain a better understanding of their dynamics. The Horqin Sandy Land in semi-arid Inner Mongolia represents one of the most severely desertified regions in China (Liu, Zhao, & Zhao, 1996). The area has been intensively grazed since 1950 and mobile dunes are widely distributed, advancing at a rate of 5–7 m year^{-1} (Wang, Jiang, Oshida, Zhou, & Miao, 2012). In this region, sand dune movement, wind erosion, and sand burial occur frequently. Using the Horqin Sandy Land mobile dunes as our study system, we set out to: (1) determine whether the soil seed bank density and species composition differs along a chronosequence (2) examine whether the similarity of the soil seed bank to above-ground vegetation changes with time, and (3) evaluate the efficacy of the soil seed bank as a source for natural vegetation restoration in inter-dune lowlands.

Materials and methods

Study area

The study was conducted in the Wulanaodu region (42°29′ ~ 43°06′N, 119°39′ ~ 120°02′E, altitude approximately 480 m) in south-western Horqin Sandy Land, Inner Mongolia, China. The study area experiences a semi-arid climate where the average annual temperature is 6.3 °C and the frost-free period extends over 130 days. 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. Average annual wind velocity varies between 3.2 and 4.5 m s^{-1}, and is dominantly from the north-west in March–May and the south-west in June–September.

Each inter-dune lowland can be seen as a self-contained unit (McLachlan et al., 1996). In some areas, the surface has stabilised as a result of vegetation growth, but elsewhere drifting sand has spread and covered previously stable surfaces (van der Hagen, Geelen, & de Vries, 2008). In the study region, a distinctive vegetation zone is generally found in lowlands larger than 1 ha (Liu et al., 2007). Sand movement, resulting in either erosion or accumulation (Fig. 1), forms zones either prone to wind erosion or sand burial, respectively. Inter-dune lowlands are very distinctive, surrounded by crescent dunes, and providing relatively good levels of moisture. Inter-dune lowlands in active dune systems show distinct vegetation zonation and are composed of four parts: wind erosion zone (Stage 1), herb zone (Stage 2), shrub zone (Stage 3) and sand burial zone (Stage 4) (Table 1, Fig. 1).

Experimental design

In early April 2011 we randomly selected three inter-dune lowlands in mobile dunes (with a vegetation cover of less than 5%). The three sites were 2.06 ha, 1.62 ha and 1.10 ha, respectively, whilst the height of the sand dunes around the slacks were all approximately equal. At each lowland site we set up three parallel transects, each running along the direction of dune movement from the leeward slope to the windward slope, ranging in lengths from 151 m at the largest site to 74 m at the smallest. We then set up 1m × 1 m quadrats along each transect. These were 3 m apart in the erosion and herb zones, and 6 m apart in the shrub and burial zones (Fig. 1). A total of 183 quadrats were set up across all sites, with 42 in Stage 1, 78 in Stage 2, 36 in Stage 3 and 27 in Stage 4. Approximate age of the entire chronosequence based on the rate of dune movement is 25 years, represented by Stage 1 (0–3 years), Stage 2 (4–7 years), Stage 3 (8–20 years) and Stage 4 (20–25 years).

Above-ground vegetation sampling

Species composition and abundance were recorded in each quadrat in August 2011, during the peak of the growing season. The percentage cover of all species within each quadrat was recorded, and was determined by visual assessment (Kim & Yu, 2009). Additionally, we estimated 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. Frequency of each

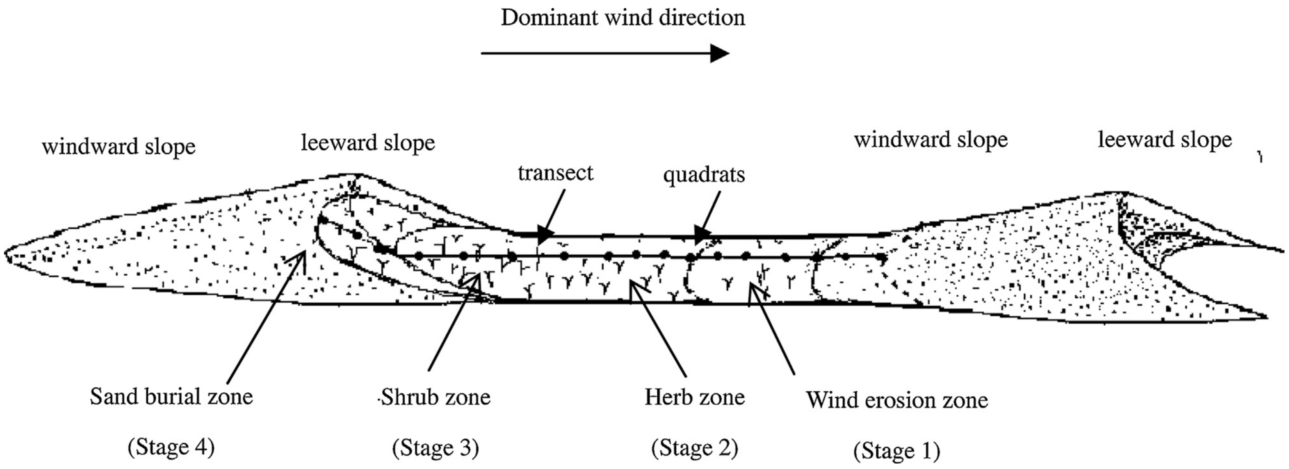

Fig. 1. A sketch map of the active sand dune system and the layout of the transects and quadrats established at each site (modified from Liu et al., 2007). Stage 1 is the wind erosion zone, followed by the herb zone (Stage 2), the shrub zone (Stage 3) and the sand burial zone (Stage 4). The main arrow indicates the dominant wind direction.

Table 1. Descriptions of the Stages represented in the active dune and inter-dune lowlands.

	Vegetation cover[a] (%)	Characteristic vegetation elements
Stage 1	<15	Only a few pioneering plant species such as *Agriophyllum squarrosum* or *Artemisia wudanica*
Stage 2	30–40	Many perennial herb and grass species such as *Phragmites communis*, *Carex duriuscula* or *Juncellus serotinus*
Stage 3	60–70	*Salix gordeivii* and *Salix microstachya* bushes of >2 m in height
Stage 4	50–60	Many annual herb and perennial herb species such as *S. viridis* and *Inula salsoloides*

[a] Cover abundance of vegetation within plots at each Stage.

species was determined using data from all transects within each inter-dune lowland site (Liu et al., 2007).

Seed bank sampling

Soil cores were collected in early April 2011, after winter stratification but before emergence of early spring annuals. Using a 7 cm diameter soil corer, soil samples were collected close to every quadrat to a depth of 10 cm. To gain an understanding of the seed bank structure, the soil cores were divided into upper layer (0–5 cm) and deep layer (5–10 cm) sections. A total of 366 soil cores were sampled for seed bank analysis, covering a total area of 1.41 m^2. The seed bank was first assessed by monitoring seedling emergence (Thompson & Band, 1997). Each soil sample was air dried and then sieved to remove stones, roots and rhizomes, before being spread out in a 16 cm diameter plastic tray in an unheated greenhouse. The trays were then watered as required over a period of 90 days (June 2011 to September 2011) and regularly inspected for emerging seedlings; these seedlings were identified, counted and removed as soon after emergence as possible. Any seedlings that could not be identified at the seedling stage were removed and grown on until identification was possible. After completion of the experiment, the samples were air-dried again and sieved through a 0.5 mm mesh. The remaining seeds were extracted, and viability was tested by staining the seeds with tetrazolium chloride. Only viable seeds were used to assess the composition and density of soil seed banks.

Data analyses

The differences in the average vegetation density and average seed density at different stages were compared by LSD test for significance ($P < 0.05$) with one-way ANOVA (Wu, Du, Liu, & Thirgood, 2009), with data obtained from each site used as replicates. All data analyses were performed using SPSS version 16.0 (SPSS for Windows, Version 16.0, Chicago, Illinois, USA). Importance values (IV) of species in plant communities at different stages were calculated as the mean of the relative density, relative frequency and relative dominance,

$$IV = (A + B + C)/3$$

where, A, B and C are the mean of relative density, relative frequency and relative dominance in plant communities at different stages, respectively (Mata, Moreno-Casasola, Madero-Vega, Castillo-Campos, & Warner, 2011; Zhang et al., 2005;). The last three indices were calculated using the following equations:

Relative density (A) = (number of individuals of a species/total number of individuals) × 100

Relative frequency (B) = (frequency of a species/sum frequencies of all species) × 100

Relative dominance (C) = (total cover for a species/total cover for all species) × 100

Detrended correspondence analysis (DCA) (Plassmann, Brown, Jones, & Edward-Jones, 2009; Yassir, van der Kamp, & Buurman, 2010) was used to examine similarities in species composition between stages of the vegetation and seed bank samples using presence/absence data. Additionally, Sørenson's Similarity Index was calculated to compare similarity between vegetation and the seed bank within each stage. DCAs were performed using CANOCO software (CANOCO 4.5 for Windows). The default settings in CANOCO were used for all analyses; these included axes rescaling, no species weighting and no transformations.

Results

Above-ground vegetation along the chronosequence

There were 64 species recorded in the vegetation, belonging to 16 families. Compositae, Leguminosae, and Gramineae were the most represented families, comprising 28%, 19% and 17% of the total species respectively. Of all 64 species, 36 were perennial herbs, 13 were annual herbs, and the remaining species were distributed among the other categories (Appendix A: Table 1). There were significant differences in the number of species per sample between Stage 1 and all other stages ($P < 0.001$), but no other significant differences. Species richness increased from Stage 1 to Stage 2 and decreased from Stage 2 to Stage 4. Species richness of annual, annual–biennial and perennial herbs in the above-ground vegetation increased during the first three stages following a successional trend. Biennial herb species were also found in the above-ground vegetation of the Stage 3 (Fig. 2A). The proportion of annual and annual–biennial herb species in above-ground vegetation increased during the course of succession along the chronosequence, whilst perennial herb species only increased during the first three stages. Semi-shrub and shrub species displayed a converse trend.

Using all vegetation data, we found an overall vegetation density of 227 individuals m^{-2}. The average vegetation density changed along the four stages (Fig. 3A). Average vegetation density increased from Stage 1 to Stage 3, and decreased slightly at Stage 4 (Fig. 3A). Vegetation density differed significantly between all stages ($P < 0.05$), except between Stages 3 and 4 ($P > 0.05$).

The relative Importance value (IV) for all the species in plant communities at different stages are shown in Appendix A. Of the 29 most prominent species (IV > 5), 17 showed an increase over the first three successional stages, e.g., *Chenopodium acuminatum, Chenopodium glaucum, Chenopodium aristatum, Lactuca indica, Calamagrostis epigeios, Salix gordeivii, Salix microstachya, Caragana microphylia* and some rare plants had the same tendency, e.g., *Hedysarum fruticosum*. As expected, the dominance of psammophyte and endemic species adapted to the semi-mobile dunes and mobile dunes, e.g., *Agriophyllum squarrosum* and *Artemisia wudanica*, decreased during the first three stages.

Soil seed bank composition along the chronosequence

A total of 6801 seeds were found belonging to 30 species. The combination of the emergence and seed extraction methods resulted in an additional 1398 seeds and 10 species compared to emergence alone. Of the total species, most were annual herbs or perennial herbs. The percentage of perennial herb species in the seed bank increased with time, whilst for annual herb species there was a converse trend during the first three stages (Fig. 2). Species richness increased during the first three stages, but decreased from Stage 3 to Stage 4, a pattern driven by annual herbs. Species richness of the perennial herbs increased along the chronosequence, while annual–biennial herbs and semi-shrubs were only found in the seed bank of the last three successional stages. Shrubs were only found in the second and third stages (Fig. 2B).

The overall average seed density at 0–10 cm of the seed bank was 9570 seed m^{-2} with a general increase throughout the four stages (Fig. 3B). The most abundant species in the seed bank were *Eragrostis pilosa, Setaira viridis, Chenopodium acuminatum, Chenopodium glaucum* and *Corispermum candelabrum*. The density pattern was the same for the upper (0–5 cm) and the lower (5–10 cm) soil layers, and the two layers combined. Average seed density increased from Stage 1 to Stage 3, and then decreased in Stage 4 (Fig. 3B). There were significant differences in seed density between all stages ($P < 0.01$), except between Stages 3 and 4 ($P > 0.05$).

Correlation between established vegetation and the soil seed bank

There were 64 species recorded in the vegetation and 30 species in the seed bank samples, of which 26 occurred in both the vegetation and the seed bank (Appendix A: Table 1). Detrended correspondence analysis (DCA) of the soil seed bank subplots and vegetation quadrats identified groupings of species composition (Fig. 4). The above-ground vegetation showed an obvious tendency along the first DCA axis, which was significantly correlated with chronosequence age. It indicated that although zones tended to cluster, there is considerable overlap in community composition for some zones, especially vegetation quadrats in Stage 4. The highest dissimilarity was found between Stages 1 and 3 (Fig. 4A). The seed bank subplots displayed no shift in community composition along the chronosequence, but the communities

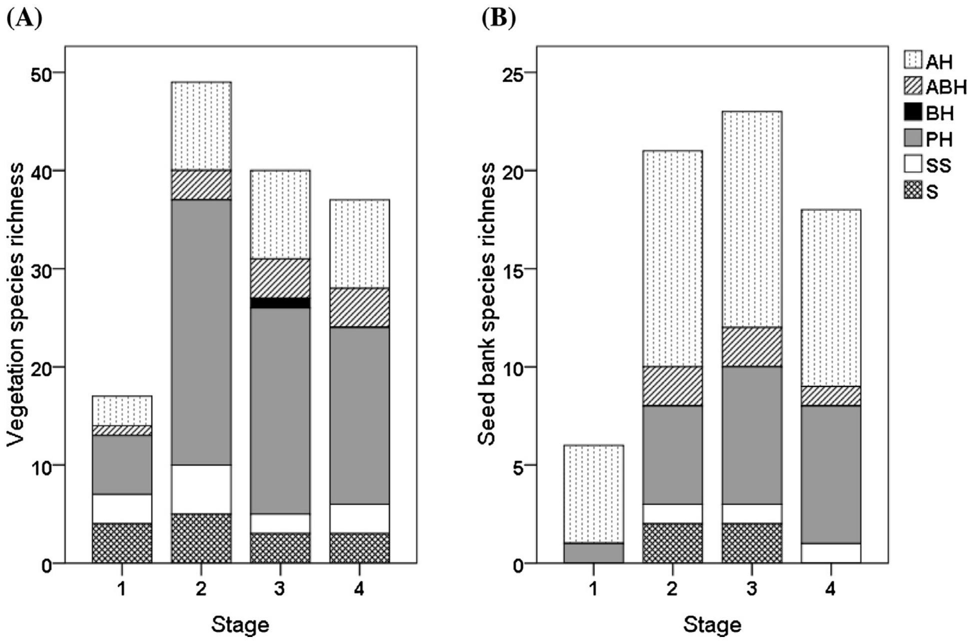

Fig. 2. Species richness at different stages in the established vegetation (A) and the soil seed bank (B). Stages are indicated by numbers (1) to (4). Key to legend codes are: AH = annual herb, ABH = annual–biennial herb, BH = biennial Herb, PH = perennial herb, SS = semi-shrub, S = shrub.

were more depauperate than their vegetation counterparts (Fig. 4B). Sørenson's Similarity Index (SSI) showed that species overlap increased with chronosequence age, from Stage 1 to Stage 4 (0.04, 0.16, 0.25, 0.26 respectively). The DCA results indicated that vegetation and soil seed bank communities overlapped more in Stages 1 and 4 than at other stages, highlighting that composition of the seed bank was more similar to the vegetation at these, than in the other stages (Appendix A: Fig. 1). The overlap in Stage 1 was driven by *Agriophyllum squarrosum*, with SSI doubling (from 0.04 to 0.08) when calculated only using quadrats where this species was present.

Discussion

Vegetation change along the chronosequence

In contrast to coastal dune systems, little information is available on species from inland dune systems in semi-arid

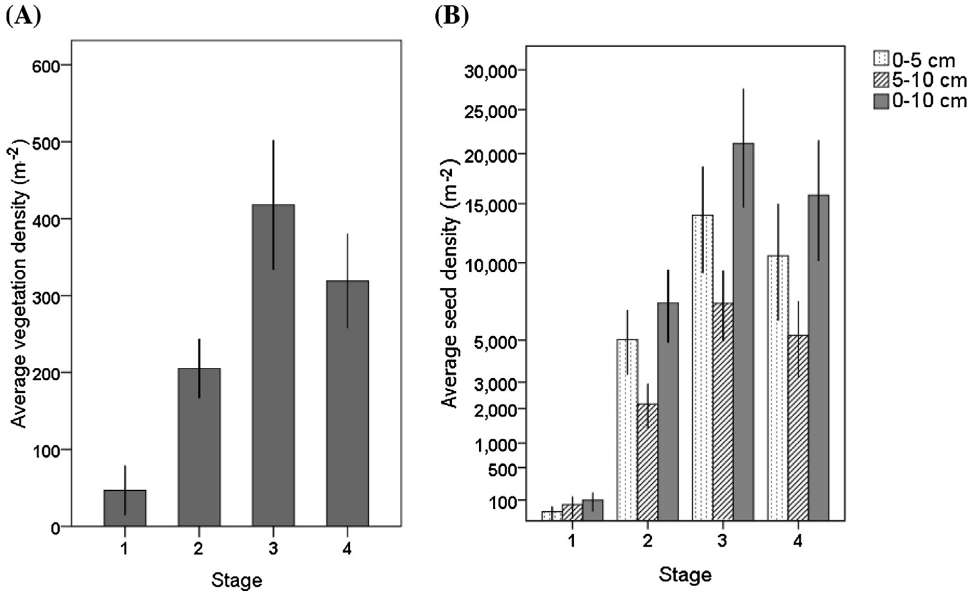

Fig. 3. Average number of plants (A) and seed density (B) per m^2 at different stages. Stages are indicated by numbers (1) to (4). Error bars are ± 1 standard error.

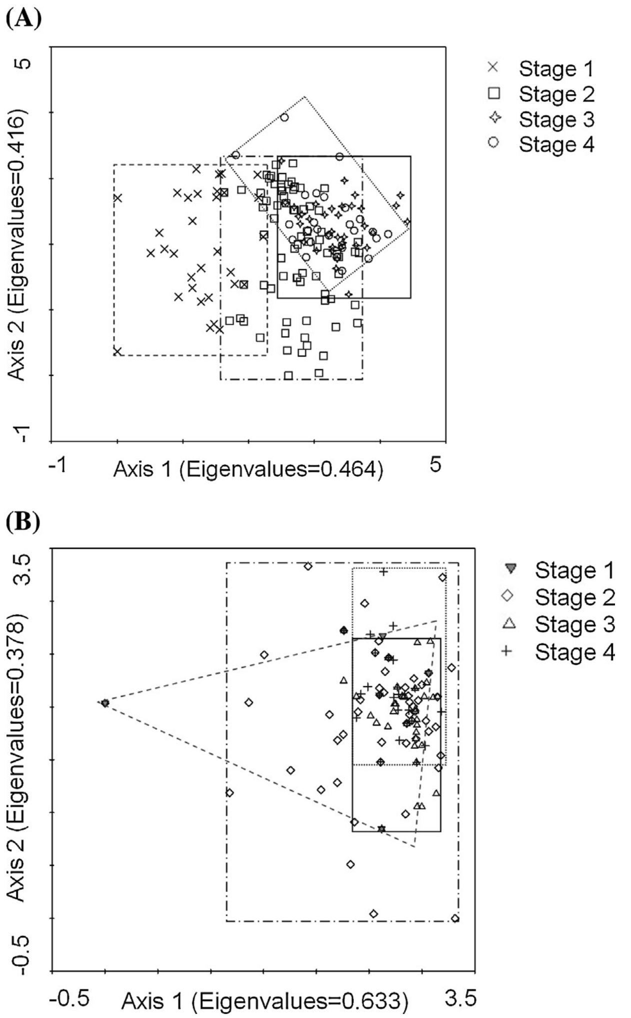

Fig. 4. Detrended Correspondence Analysis (DCA) of species composition in 183 above-ground vegetation quadrats (A) and 183 seed bank (subplots B) at four different stages along the chronosequence. Stages are indicated by numbers (1) to (4).

regions. The number of species recorded were lower than in many coastal studies, and the composition of growth forms was skewed towards perennial and annual herbs. Several factors could explain the richer species diversity at coastal sites. Firstly, hydrological conditions on the coast have a strong effect, with pioneer species supported by mineral-rich, high pH ground water, and the subsequent build-up of organic matter stimulating the growth of strong competitors and tree species (Grootjans, Hartog, Fresco, & Esselink, 1991). Nutrient-rich habitats, such as marshes and grasslands, also play an important role in determining the species diversity in many of these systems (Bossuyt et al., 2005b). In contrast, the Horqin Sandy Land system has resulted from the long-term degradation of the steppe woodland, and the species richness is a reflection of desertification and subsequent succession, based on simplified plant community structure of sand- and/or salt-tolerant species (Jiang, Kou, Li, & Li, 2009).

The relationship between plant community development over time and dune habitat development in coastal dune systems is well established (e.g., Ernst, Slings, & Nelissen, 1996; Pegman & Rapson, 2005; Sýkora, van den Bogert, & Berendse, 2004) and our study supports this. Community structure and composition were clearly evident as age-related differences in each of the stages. For e.g., dominance in Stage 1 of *Agriophyllum squarrosum* and *Artemisia wudanica*, adapted to the semi-arid climate and mobile dunes, decreased during the first three stages, indicative of the role that shrubs play as psammophytes in these habitats. On the other hand, species richness across all growth forms increased significantly from the species-poor Stage 1 throughout the following Stages, peaking in Stage 2. This is an example of the tendency for species richness to peak at intermediate levels along disturbance gradients, and is likely to be a result of several factors. Firstly, whilst species richness is high, overall early stage plant density is still low, suggesting that competition also remains low. Additionally, different stages may co-exist within Stage 2 (Liu et al., 2007), with areas of emergent groundwater favouring limnocryptophytes such as *Typha orientalis* and *Juncellus serotinus*, and remnant areas of sand deposition maintaining habitat for psammophytes such as *Artemisia wudanica*.

In contrast to coastal studies (e.g., Bossuyt, Honnay & Hermy, 2005a), the oldest stage in our study displayed a noticeable decline in species richness and plant density. In part, this was due to the increased dominance of a smaller number of shrub species such as *Salix gordeivii* and *Salix microstachya*, and the increased dominance of the grass *S. viridis*. The older stages in our mobile system are prone to disturbance because of their proximity to the leeward slope of encroaching dunes and sand deposition. Additionally, the greater densities of adult plants reduce the available soil moisture and subsequent germination (Yan, Liu, Ma, & Jiang, 2007). It is therefore likely that late stages in these systems have reduced formation of depressions with emergent water (Liu et al., 2007), which reduces the available habitat for a wider range of species, resulting in an unusual successional progression where disturbance affects composition in the oldest stage.

Soil seed bank change along the chronosequence

The mean seed density in our study system was greatly influenced by the very small number of seeds held within the young mobile zone, but fell broadly within the range found in coastal studies (e.g., Bossuyt & Hermy, 2004; Plassmann, Brown, Jones, & Edward-Jones, 2009). However, the low density of seeds found in some studies may result from insufficient cold stratification of the seed bank before assessment by the emergence method (Leicht-Young et al., 2009; Plassmann et al., 2009), or the use of a greenhouse with fixed photoperiod and temperature, which may not provide the temperature fluctuations required to trigger germination in some species. As a result of the large increase in species found combining emergence and seed extraction methods, we recommend that in studies where assessment using seasonal conditions or long-term monitoring of emergence isn't possible, additional seed extraction may improve estimation of seed bank composition and density.

In each stage of our study, more than half of the seeds recorded belonged to only a few species (e.g., *Eragrostis pilosa, S. viridis* across all Stages and *Agriophyllum squarrosum* in Stage 1). This suggests that seed banks of several of the most common species, particularly pioneer psammophytes, are persistent. Studies investigating the dormancy and germination requirements of these species support this hypothesis. For e.g., *Agriophyllum squarrosum* maintained a proportion of dormant seeds at alternating temperatures of 15/5 °C as well as a dark requirement for germination across all temperatures tested (Zheng, Gao, Ping, Shimizu, & Rimmington, 2004). Species richness dominated by annual herb species through all four stages, irrespective of the above-ground vegetation composition is also a strong indication of persistent seed banks maintained by species with this growth form.

Fewer seeds were found in the surface layer (0–5 cm) than in the deeper layer (5–10 cm) in Stage 1, albeit at extremely low overall density levels. The other three stages displayed a complete reversal, with approximately half the number of seeds found in the deeper than the surface layers. This latter result is the most commonly reported (e.g., Bekker, Lammerts, Schutter, & Grootjans, 1999; Bossuyt & Hermy, 2004; Plassmann et al., 2009), in part because of the focus of studies on fixed dune areas. Perhaps not surprisingly, studies that investigate the earliest successional stages, find vastly different mechanisms controlling seed bank dynamics. It has been postulated that due to limited structures available to trap seeds, light seeds are easily blown away from the surface by strong winds (Yan et al., 2007). Also, seeds exposed to the surface by sand erosion have access to better levels of soil moisture, facilitating germination, and depleting the seed bank in the upper layer (Grubb, 1988).

Five of the eight rare or endemic species were present in the soil seed bank suggesting it provides some capability for restoration of this group. Several rare species belonged to the Leguminosae, and would have physical dormancy and a persistent seed bank. Two species not present in the seed bank were the dominant shrubs *Salix gordeivii* and *Salix microstachya*, which depend more on long-distance dispersal and fast germination and growth (Yan et al., 2007), rather than persistence in the soil.

Correlations of seed bank and vegetation, and relevance for restoration

Seed bank density and species richness correlated strongly with the above-ground vegetation, however, there were fewer species present in the seed bank. Conversely, species represented in the seed bank were almost always present in the above-ground vegetation, as has been found in other studies (Bossuyt & Hermy, 2004; Bossuyt, Stichelmans, & Hoffmann, 2005b; Plassmann et al., 2009). Even though there was a positive correlation between perennial herb species richness and perennial herb species density in the seed bank and vegetation, the overall dissimilarity appeared to be driven by perennial species.

Annual herb species were the dominant growth form in the seed bank across all four stages and maintained the strongest correlation with above-ground vegetation. Annuals species have also been found to dominate seed banks in Mediterranean salt-marsh habitats (Marañón, 1998). Annual herbs produce large quantities of seeds, which often have a high longevity index (Plassmann et al., 2009), a capacity for fast dispersal (Bossuyt & Hermy, 2004; Thompson, 1987), and allocate a higher fraction of their resources to seeds than their perennial counterparts (Thompson, Band, & Hodgson, 1993).

The relationship between soil seed banks and the established vegetation is crucial for evaluating the role of seed banks in revegetation potential (Lu, Li, Jiang, Huang, & Bao, 2010). The correlation between seed bank and vegetation at Stages 1 and 4 may be a result of the frequency of sand movement, particularly in Stage 1, which is dominated by *Agriophyllum squarrosum*. In later stages, above-ground vegetation dominated by perennials contributes to a lack of correlation between the seed bank and established vegetation, however, annual species correlate well. Our findings differ from seed bank studies of many coastal dune systems, where the seed bank is not considered the dominant source for the establishment of species following disturbances (Bakker, de Graaf, Ernst, & van Bodegom, 2005) and unlikely to be a driving force in successional change (Bossuyt & Hermy, 2004; Bossuyt et al., 2005b).

It is clear that the amount of data available up to now on established vegetation and its relationship with the soil seed bank in inland dune systems is very limited, especially for the inter-dune lowlands of active dune fields in semi-arid regions. We conclude that the seed bank could play a key role in the establishment of early stage successional species, particularly the dominant pioneer psammophyte *Agriophyllum squarrosum*. Large seed production, morphology and long-term seed persistence (up to 25 years) of this pioneer species all contribute to its ability to establish on mobile sands (Yan et al., 2005; Zheng et al., 2004). In addition, higher similarity between the soil seed bank and vegetation at earlier stages, as has been found in other studies (e.g., Bekker et al., 1999; Plassmann et al., 2009; van der Hagen et al., 2008), contributes to the conclusion that establishment of the vegetation could be facilitated by the soil seed bank. In later stages, the high seed density we found is similar to that of nearby inter-dune areas that had been enclosed for 10 years, as part of management efforts to reduce degradation (Zhao, Li, Zhao, Zhao, & Zhao, 2006). This suggests that the seed bank could contribute to maintaining species diversity as part of the restoration process, particularly for the establishment of annual species which was the most highly represented group.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.baae.2015.04.010.

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