Full Title: Sand dune stabilization changes the vegetation characteristics and soil seed bank and their correlations with environmental factors

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ABSTRACT

Currently the amount of data available on the effect of sand dune stabilization on species conservation in inter-dune lowland is very limited, especially for the sand dune systems in semi-arid regions. In this study, we determined whether the characteristics of above-ground vegetation, soil seed bank and their relationships with environmental factors changed with sand dune stabilization in the inter-dune lowlands in Horqin Sandy Land, China. Species composition, abundance and coverage of aboveground vegetation as well as soil seed bank composition and density were surveyed and their correlations with environmental factors (pH, organic matter content, total nitrogen and total phosphorus) were determined. The results showed that changes in the relationship between aboveground vegetation, soil seed bank and soil quality followed the changes in aboveground vegetation and soil seed banks. Aboveground vegetation species richness increased with sand dune stabilization, but soil seed bank species richness declined. The inter-dune lowland of active sand dunes could provide specific habitats for some endemic species and pioneer psammophyte species as indicated by data on aboveground vegetation and soil seed bank. Our results suggested that both active and stabilized sand dunes should be maintained since active sand dunes are essential for the survival of endemic or pioneer species and stabilized sand dunes are important for sustaining species richness.

Keywords: Inter-dune lowland; Active sand dune; Endemic species; Semi-arid ecosystem; Restoration

1. Introduction

Sand dune mobility in desert ecosystems reflects the underlying ecological processes, including biotic interactions, seed dispersal, vegetation succession, and environmental change (Fan et al., 2017; Hao et al., 2017). Population pattern in sand dunes is a result of long term interactions between living vegetation and seed bank as well as their relationships with the environment (Zhang et al., 2015). Previous studies have shown that dune stabilization in semi-arid areas has led to distinct dune habitat types. For example, sand pioneer plants are the dominant species in barren soils of active dunes, and herbaceous plants are the dominant species in the stabilized dunes (Zuo et al., 2008; Yan and Liu, 2010). Over time, stabilization and the accumulation of organic material increase available nutrients and stimulate 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 and decreased sand movement (Pake and Venable, 1996).

Horqin Sandy Land located in the semi-arid of southeast Inner Mongolia, China, is one of the most severely desertified regions in China (Liu et al., 1996; Wang et al., 2016). Therefore, different artificial acceleration regeneration methods have been adopted to promote sand dune stabilization in the last 40 years, such as building physical sand barriers and excluding livestock grazing. By conducting these methods, some mobile dunes can also be gradually restored to semi-stabilized or stabilized dunes (Zuo et al., 2014), including the interdune lowlands which provide refuge for a relatively large number of rare and endangered species (Gunster, 1994) such as invertebrates, amphibians, and other wildlife (McLachlan et al., 1996; Everard et al., 2010). Surrounded by crescent dunes, they provide relatively sufficient levels of moisture and generally have better soil condition than the surrounding sand dunes.

Vegetation and seed bank are the most important biotic components in sand dune habitat as they have direct and indirect impacts on the stability and resilience of dune structure (Wang et al., 2015). Vegetation is integral to dune structure as it facilitates accretion and stabilization (Yan et al., 2009; Liu et al., 2012). Currently there are two contrasting ecological perspectives on sand dune stabilization. One favors dune stabilization due to its positive influence of plant diversity (Zuo et al., 2014), while the other considers dune stabilization to have adverse impacts on endemic and pioneer species due to pioneer species adapting to unstable substrate (Yan and Liu, 2010). However, our knowledge on how the characteristics of above-ground vegetation and soil seed bank and their correlations with environmental factors change in the inter-dune lowlands in Inner Mongolia, China is still lacking, including the effects of sand dune mobility that have been known to influence vegetation and soil seed bank patterns in inter-dune lowland (Liu et al., 2007). The influence of environmental factors on the variations in plant diversity and community composition is also unknown, despite their importance for understanding ecological patterns and processes (Zuo et al., 2014), as well as for providing management decisions for conservation or restoration measures (McLachlan et al., 1996). We therefore conducted a series of field surveys and specifically asked the following questions: (1) Do the characteristics of above-ground vegetation and soil seed bank change with sand dune stabilization? (2) How do the environmental characteristics change with sand dune stabilization? (3) How do the relationships between vegetation, soil seed bank and environmental factors change with sand dune stabilization? We hypothesized that the characteristics of above-ground vegetation and soil seed bank and their correlations with environmental factors would change with sand dune stabilization.

2. Materials and methods

2.1. Study area

The study was conducted at the Wulanaodu region (42°29′-43°06′N, 119°39′-120°02′E, altitude approx. 480m) in south-western Horqin Sandy Land, 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 340.5mm, 70% of which falls between June and September and the frost-free period extends over 130 days. The average annual wind velocity varies between 3.2 and 4.5m s^{-1}, and is dominantly from the north-west in March - May and the south-west in June - September. The area has been intensively grazed since 1950, thus, overgrazing is the major force leading to its desertification. Active dunes (AD), stabilized dunes (SD) and the inter-dune lowland are distributed in mosaics. Similarly, the pattern of natural vegetation is characterized by a mosaic of grasslands and sand dunes, including the flood plain grasslands, lowland grasslands, meadows, stabilized dunes, semi-stabilized and active dunes (Zuo et al., 2012).

2.2.Experimental design and data collection

In early April 2011 we randomly selected several inter-dune lowlands and set up 6 sticks in each inter-dune lowland to monitor sand dune movement. After one year monitoring, in early April 2012, four inter-dune lowlands were randomly selected, two in AD and the other two in SD. The height of the sand dunes around the inter-dune lowlands were all approximately equal. At each lowland site we set up two parallel transects, each running along the direction of dune movement from the leeward slope to the windward slope. Then we set up 2m×2m quadrats along each transect; distance between quadrats was 5 m apart. A total of 94 quadrats were set up across all sites. There were more quadrats in AD (58) compared to SD (36) because the length of the transects along the direction of dune movement from the leeward slope to the windward slope were different between AD and SD.

2.3. Above-ground vegetation investigation

Species composition and abundance were recorded in each quadrat at the end of July and August 2012, during the peak of the growing season. Percentage cover of all species within each quadrat was recorded using visual assessment. 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, whereas for clonal species we counted the number of ramets. For species with discrete individuals, we counted the number of individuals. Frequency of each species was determined using data from all transects within each inter-dune lowland (Liu et al., 2007).

2.4. Seed bank sampling

Soil cores were collected in early April 2012, after winter stratification but before the emergence of early spring annuals. Using a 7 cm diameter soil corer, soil samples were collected close to every quadrat (subplots) to a depth of 10 cm; each was divided into upper layer (0–5 cm) and deep layer (5–10 cm) section to estimate soil seed bank composition. A total of 188 soil cores were sampled for seed bank analysis, covering a total area of 0.72 m^2. The seed bank was first assessed by monitoring seedling emergence (Thompson and 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 over a period of 90 days (June 2012 to September 2012) 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. At the end of 90-days period, soil samples were air-dried and sieved through a 0.5 mm mesh to extract the remaining seeds. Their viability was then tested using tetrazolium chloride. Only viable seeds were used to assess the composition and density of soil seed banks.

2.5. Soil physicochemical characteristics

Ten soil samples were taken near each quadrat (core diameter 7.0 cm, depth 10 cm) in August 2012. These samples were first pooled and the soil samples were prepared by quartering. Each quartered soil sample was air-dried and then sieved through a 2 mm screen to remove stones, roots and rhizomes. Large aggregates were gently processed by hand during the screening procedure. Sample splitting method, by which a desired sample size was achieved by repeating coning and quartering, was applied to a total of 94 soil samples before bringing them to laboratory for further analysis. Soil pH was measured by using a potentiometer, organic matter content (soil organic carbon) by potassium dichromate heating method, total nitrogen by Kjeldahl procedure, and total phosphorus by Mo-Sb colorimetric method.

2.6. Statistical analyses

One-Way ANOVA was used to compare vegetation characteristics (density, coverage), soil seed bank characteristics (density), and soil chemical properties (pH, organic matter, total N, total P, and C/N ratio). 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 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 (Zhang et al., 2005; Mata et al., 2011). 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,

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

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

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

Relative density (A) = (number of seed of a species/total number of seed) x 100.

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

Simpson diversity index (D): $D = 1 - \sum P_{\mathrm{i}}^2$,

Shannon-wiener Index (H): $H = -\sum(P_i \ln P_i)$,

Pielou index (J): $E = \mathrm{H}/\ln S$,

where P_i is the relative importance value of species i, and S the total number of species.

Detrended Correspondence Analysis (DCA) (Plassmann et al., 2009; Yassir, van der Kamp and Buurman, 2010) was used to examine similarities between vegetation and the soil seed bank in the inter-dune lowlands of AD and SD. Canonical Correlation Analysis (CCA) and Redundancy Analysis (RDA) was used to examine of the correlations between vegetation, soil seed bank and environmental factors in the inter-dune lowlands of AD and SD. DCAs, CCA and RDA were performed using CANOCO software (CANOCO 4.5 for Windows). The default settings in CANOCO were used for all analyses; these included axis rescaling, no species weighting, and no transformations.

3. Results

3.1. Characteristics of above-ground vegetation

There were 44 vegetation species recorded in the inter-dune lowlands of AD and 59 species recorded in the inter-dune lowlands of SD, 32 of which occurred in both inter-dune lowlands of AD and SD (Table 1). The coverage was 61% in the inter-dune lowlands of AD and 89% in the inter-dune lowlands of SD, and there were significant differences between the inter-dune lowlands of AD and SD ($P<0.01$; Table 1). The average vegetation densities were 149 and 233 individuals m^{-2} in the inter-dune lowlands of AD and SD, respectively, and there were significant differences between the inter-dune lowlands of AD and SD ($P<0.05$; Table 1).

Overall, total species richness, coverage and average vegetation density of above-ground vegetation in the inter-dune lowlands of AD were lower than the inter-dune lowlands of SD (Table 1). Perennial herbs were the most diverse life form in both SD and AD while annual herbs were the most abundant individuals in the area (Fig. 1a). There were little differences of Simpson diversity index (D), Shannon-wiener Index (H) and Pielou index (E) between the inter-dune lowlands of AD and SD (Table 1).

3.2. Characteristics of soil seed bank

Twenty-three species were found in the soil seed bank at 0-10 cm in the inter-dune lowlands of AD and 19 species were found in the inter-dune lowlands of SD, with 15 species occurred in both the inter-dune lowlands of AD and SD (Table 2). The average seed bank densities at 0-10 cm were 11599 and 7074 seeds m^{-2} in the inter-dune lowlands of AD and SD, respectively ($P > 0.05$), and there were significant differences between the inter-dune lowlands of AD and SD at 5-10 cm soil layer ($P=0.01$, Table 2). Higher seed density was found in upper layer (0-5 cm) than in lower layer (5-10 cm) for both AD and SD, although overall there was higher seed density in AD than SD (Table 2). Of the total species in soil seed bank of AD and SD, annual herbs and perennial herbs species was the majority, whereas for seed density, the most abundant species was annual herbs (Fig. 1b). Simpson diversity index (D), Shannon-wiener Index (H) and Pielou index (E) of the seed bank in the inter-dune lowlands of AD were much higher than in the inter-dune lowlands of SD (Table 2).

3.3.Soil properties

Organic matter, total nitrogen, total phosphorus and pH were significantly different between the inter-dune lowlands of AD and SD ($P<0.01$, Table 3). Organic matter, total nitrogen, total phosphorus and pH in the inter-dune lowland of SD were higher than the inter-dune lowland of AD, while the contrasting trend was found for C/N.

3.4.Correlation between established vegetation and the soil seed bank

There were 44 species recorded in vegetation and 23 species in the seed bank samples, 17 of which occurred in both the vegetation and the seed bank in the inter-dune lowland of AD. Meanwhile, there were 59 species recorded in vegetation and 19 species in the seed bank samples, 15 of which occurred in both the vegetation and the seed bank in the inter-dune lowland of SD (Table 4). Established vegetation and soil seed bank were most similar for annual herbs compared to other growth forms, both in the inter-dune lowland of AD and SD (Table 4).

The Detrended Correspondence Analysis (DCA) of the soil seed bank and vegetation quadrats indicated that vegetation and soil seed bank communities more overlapped in both the inter-dune lowland of AD and SD, highlighting that composition of the soil seed bank was more similar to the vegetation (Fig. 2). AH and PH were most dominant in plant communities in the inter-dune lowland of AD, with total importance values of 39.79% and 32.83%. The total importance values of AH and PH were 37.26% and 34.54% for plant communities in the inter-dune lowland of SD, which were similar to those in AD. For soil seed bank, AH was the most dominant species, with total importance values of 97.71% and 92.33% in the inter-dune lowland of AD and SD (Table 4). The endemic plant species (e.g., *Artemisia wudanica*) were only recorded in the inter-dune lowland of AD. The importance values of all psammophyte species in AD were much higher than in those SD for both plant communities and soil seed banks (Table 4).

3.5. Correlation between vegetation, soil seed bank and environmental factors

The CCA results indicated that there was a converse trend between the established vegetation in the inter-dune lowland of AD and SD. The established vegetation in the inter-dune lowland of AD had positive correlation with C/N, while the established vegetation in the inter-dune lowland of SD had positive correlation with OM, TN, pH and TP (Fig. 3a). Meanwhile, the RDA results indicated that there was a converse trend between the soil seed bank in the inter-dune lowland of AD and SD. Soil seed bank in the inter-dune lowland of AD had positive correlation with C/N, but soil seed bank in the inter-dune lowland of SD had positive correlation with pH, TP, OM and TN (Fig. 3b).

4. Discussion

4.1. Sand dune stabilization changes the characteristics of above-ground vegetation

Our data suggested that total species richness, and coverage, as well as average vegetation density of above-ground vegetation in the inter-dune lowlands of AD were lower than those in the inter-dune lowlands of SD (Table 1). These findings were consistent with earlier reports that inter-dune lowlands of AD have low productivity and low species diversity (Zuo et al., 2012), and that species richness in stabilized dunes is higher than that in active dunes (Yan and Liu, 2010). Generally, the establishment of vegetation gradually limits sand transport (Okin et al., 2006; Xu et al., 2015). During the stabilization processes from AD to SD, changes in chemical and physical properties of topsoil (e.g., increasing fine soil particles) enhance soil restoration processes (Zuo et al., 2008). Soil organic C, total N and total P increase significantly in the upper soil layer (Su et al., 2005), increasing the density of annual and perennial herbs (Fig. 1a). The associated increase in vegetation density can further buffer a dune system by preventing wind erosion (Tanaka et al., 2009), favoring plant establishment (Liu et al., 2014; Xu et al., 2015).

Annual herbs were the most abundant species in terms of vegetation density (Fig. 1a). Because annual plants can produce more seeds per unit ground area than large-seeded species, they have an advantage over perennial plants during seed production (Moles et al., 2004). Although some researchers consider that dunes populated by diverse vegetation species are more stable than areas with sparse or no vegetation (Wootton et al., 2003), other researchers have different opinion. Reiss et al. (2009) for example showed species richness does not necessarily equate to functional diversity which can enhance ecosystem processes.

4.2. Sand dune stabilization changes the characteristics of soil seed bank

Seed availability may be the key limiting factor of population recruitment and vegetation restoration in sand dune ecosystems (Guardia et al., 2000). In our study, total species richness and seed density of soil seed bank in the inter-dune lowlands of AD were higher than those in the inter-dune lowlands of SD (Table 2). Generally, the relatively weak aeolian activities on the stabilized sand dune means that fewer seeds can be transported, whilst for the active sand dune, much more seeds can be transported into the inter-dune lowland (Qian et al., 2016). Some authors found the same trend that the density of soil seed bank increases with degree of disturbance (Ma et al., 2010; Quintana-Ascencío and Menge, 1996).

Soil seed bank richness of AD and SD was dominated by annual herbs and perennial herbs, whereas annual herbs dominated soil seed bank density (Fig. 1b). Similar to these findings, annual species have also been found to dominate seed banks in Mediterranean salt-marsh habitats (Marañón, 1998). Life history and seed size are closely related to seed bank formation (Honda, 2007). Since annual herbs produce large quantities of small seeds that can easily enter into deep soil (Thompson et al., 1993), they often have a high longevity index (Plassmann et al., 2009, Wang et al., 2015). Annual herbs also allocate a higher fraction of their resources to seeds than their perennial counterparts and have a capacity for fast dispersal (Thompson, 1987; Bossuyt and Hermy, 2004).

4.3. Sand dune stabilization changes the characteristics of environmental factors

Our result showed that organic matter, total nitrogen, total phosphorus and pH in the inter-dune lowland of SD were higher than the inter-dune lowland of AD （$P<0.01$）, and the reverse was found for C/N (Table 3). As nutrients and organic matter accumulate with time, they increase species complexity along the following successional stages (Gerlach et al., 1994; Tackett and Craft, 2010). First, soil wind erosion rate decreases with increasing vegetation coverage. At the same time, roots also hold the soil in place, increasing the stability of soil matrixes. Then, the accumulated litter covers the soil and increases soil organic matter content and permeability, reduces runoff, and extends runoff time.

4.4. Sand dune stabilization changes the relationship between vegetation and soil seed bank

We observed that species composition of both the above-ground vegetation and soil seed bank changed differently with sand dune stabilization. The aboveground vegetation species richness increased, but soil seed bank species richness declined with sand dune stabilization (Table 4), similar to observation of other authors (Yan et al., 2009; Yan and Liu, 2010; Qian et al., 2016). We also found that the inter-dune lowland of active sand dunes could provide specific habitats for some endemic species and pioneer psammophyte species such as *Artemisia wudanica* and *Agriophyllum squarrosum*, similar to findings of Liu et al., (2007) and Qian et al., (2016). The results of this study suggested that seed banks of a heavily degraded inter-dune lowland still contained an abundant mix of pioneer and early successional plant propagules, which potentially contribute to the endemic and rare pioneer species establishment in semi-arid sand area (O'Donnell et al., 2016). Additionally, we found that the composition of the seed bank was high similar to the aboveground vegetation (Fig. 2). Annual herb species were the dominant growth form in the seed bank in the inter-dune lowland of AD and SD, and contributed to a strong correlation with above-ground vegetation (Table 4). We concluded that the seed bank could play a key role in the establishment of vegetation species, particularly the dominant pioneer psammophyte and the annual herb species.

4.5. Sand dune stabilization changes the correlations of above-ground vegetation, soil seed bank and environmental factors

In the process of desertification in the Horqin Sandy Land, changes in the habitat of sandy grasslands have an important influence on the formation of community and invasive species (Zuo et al., 2012). Soil nutrient are the main factor controlling sandy vegetation community pattern, while the micro-habitats determine the final plant community structure. At the same time, species diversity can also indicate the environmental conditions. In our study, the established vegetation and soil seed bank in AD was positively correlated with C/N, but negatively correlated with pH, organic matter, total nitrogen and total phosphorus (Fig. 3). With lower pH, organic matter, total nitrogen and total phosphorus, the inter-dune lowlands of AD were more suitable for the species of the aboveground vegetation and soil seed bank. However, the established vegetation and soil seed bank in SD showed the opposite trend, a positive correlation with pH, organic matter, total nitrogen, total phosphorus, but a negative correlation with C/N (Fig. 3). This indicated that above ground vegetation species and soil seed bank in the inter-dune lowland of SD grew better in soils with higher pH, organic matter, total nitrogen and total phosphorus. Overall, the changes of relationship between aboveground vegetation, soil seed bank and soil environmental quality corresponded with species changes and soil seed banks.

5. Conclusions

This study contributes towards a better understanding of sand dune stabilization by showing the changes in the characteristics of above-ground vegetation and soil seed bank, including their correlations with environmental factors. The aboveground vegetation species richness increased with sand dune stabilization. Conversely, the soil seed bank species richness declined. The inter-dune lowland of active sand dunes could provide favorable habitats for some endemic species and pioneer psammophyte species for both aboveground vegetation and soil seed bank, although aboveground vegetation species richness increased with sand dune stabilization. Therefore, both active and stabilized sand dunes should be maintained for restoration purpose in the Harqin Sandy Land, Inner Mongolia, China.

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References

Bossuyt, B., Hermy, M., 2004. Seed bank assembly follows vegetation succession in dune slacks. Journal of Vegetation Science. 15, 449–456.

Charbonneau, B.R., Wnek, J.P., Langley, J.A., Lee, G., Balsamo, R.A., 2016. Above vs. belowground plant biomass along a barrier island: Implications for dune stabilization. Journal of Environmental Management. 182, 126–33.

Everard, M., Jones, L., Watts, B., 2010. Have we neglected the societal importance of sand dunes? An ecosystem services perspective. Aquatic Conservation-Marine and Fresh water Ecosystems. 20, 476–487.

Fan, D., Zhang, Y., Qin, S., Wu, B., 2017. Relationships between *Artemisia ordosica* communities and environmental factors following sand-dune stabilization in the Mu Us desert, northwest China. Journal of Forestry Research. 28(1),115–124.

Gerlach, A., Albers, E.A., Broedlin,W., 1994. Development of the nitrogen cycle in the soils of a coastal dune succession. Acta Bot. Neerl. 43 (2), 189–203.

Guardia, R., Gallart, F., Ninot, J.M., 2000. Soil seed bank and seedling dynamics in badlands of the upper Llobregat basin (Pyrenees). Catena. 40, 189–202.

Gunster, A., 1994. Seed bank dynamics — longevity, viability and predation of seeds of serotinous plants in the central Namib Desert. Journal of Arid Environments. 28 (3), 195–205.

Hao, H.M., Huang, Z., Lu, R., Jia, C., Liu, Yu., Liu, B.R. , Wu G.L., 2017. Patches structure succession based on spatial point pattern features in semi-arid ecosystems of the water-wind erosion crisscross region. Global Ecology and Conservation. 12, 158–165.

Honda, Y., 2007. Ecological correlations between the persistence of the soil seed bank and several plant traits, including seed dormancy. Plant Ecology. 196 (2), 301–309.

Liu, B., Liu, Z., Wang, L., 2012. The colonization of active sand dunes by rhizomatous plants through vegetative propagation and its role in vegetation restoration. Ecological Engineering. 44, 344–347.

Liu, B., Liu, Z., Lü, X., Maestre, F.T., Wang, L., 2014. Sand burial compensates for the negative effects of erosion on the dune-building shrub *Artemisia wudanica*. Plant and Soil. 374 (1-2), 263–273.

Liu, B., Liu, Z., Wang, L., Wang, Z., 2014. Responses of rhizomatous grass Phragmites communis to wind erosion: effects on biomass allocation. Plant and Soil. 380 (1-2), 389–398.

Liu, Z.M., Yan, Q.L., Liu, B., Ma, J.L., Luo, Y.M., 2007. Persistent soil seed bank in *Agriophyllum squarrosum* (Chenopodiaceae) in a deep sand profile: variation along a transect of an active sand dune. Journal of Arid Environments. 71, 236–242.

Liu, X.M., Zhao, H.L., Zhao, A.F., 1996. Windy and sandy environment and vegetation in Horqin Sandy Land. Beijing: Chinese Science Press.

Liu, Z.M., Li, X.L., Yan, Q.L., Wu, J.G., 2007. Species richness and vegetation pattern in interdune lowlands of an active dune field in inner Mongolia, China.

Biological Conservation. 140, 29–39.

Ma, M., Zhou, X., Du, G., 2010. Role of soil seed bank along a disturbance gradient in an alpine meadow on the Tibet plateau, Flora. 205, 128–134.

Mata, D.I., Moreno-Casasola, P., Madero-Vega, C., Castillo-Campos, G., Warner, B.G. 2011. Floristic composition and soil characteristics of tropical fresh water forested wetlands of Veracruz on the coastal plain of the Gulf of Mexico. Forest Ecology and Management. 262, 1514–1531.

Marañón, T., 1998. Soil seed bank and community dynamics in anannual-dominated Mediterranean salt-marsh. Journal of Vegetation Science. 9, 371–378.

McLachlan, A., Kerley, G., Rickard, C., 1996. Ecology and energetics of slacks in the Alexandria coastal dunefield. Landscapeand Urban Planning. 34, 267–276.

Moles, A.T., Falster, D.S., Leishman, M.R., Westoby, M., 2004. Small-seeded species produce more seeds per square metre of canopy per year, but not per individual per lifetime. Journal of Ecology. 92, 384–396.

O'Donnell, J., Fryirs, K.A., Leishman, M.R., 2016. Seed banks as a source of vegetation regeneration to support the recovery of degraded rivers: A comparison of river reaches of varying condition. Science of the Total Environment. 542, 591–602.

Okin, G.S., Gillette, D.A., Herrick, J.E., 2006. Multi-scale controls on and consequences of aeolian processes in landscape change in arid and semi-arid environments. J. Arid Environ. 65, 253–275.

Pake, C.E., Venable, D.L., 1996. Seed banks in desert annuals: Implications for persistence and coexistence in variable environments. Ecology. 77, 1427–1435.

Plassmann, K., Brown, N., Jones, M.L.M., Edwards-Jones, G., 2009. Can soil seed banks contribute to the restoration of dune slacks under conservation management? Applied Vegetation Science. 12, 199–210.

Qian, J., Liu, Z., Hatier, J.H.B., Liu, B., 2016. The vertical distribution of soil seed bank and its restoration implication in an active sand dune of northeastern Inner Mongolia, China. Land Degradation & Development. 27 (2), 305–315.

Quintana-Ascencío, P.F., Menge, E.S., 1996. Inferring metapopulation dynamics from patch-level incidence of Florida scrub plants. Conserv. Biol. 10, 1210–1219.

Reiss, J., Bridle, J.R., Montoya, J.M., Woodward, G., 2009. Emerging horizons in biodiversity and ecosystem functioning research. Trends Ecol. Evol. 24 (9), 505–514.

Su, Y.Z., Li, Y.L., Cui, J.Y., Zhao, W.Z., 2005. Influences of continuous grazing and livestock exclusion on soil properties in a degraded sandy grassland, Inner Mongolia, northern China. Catena. 59, 267–278.

Tackett, N.W., Craft, C.B., 2010. Ecosystem development on a coastal barrier island dune chronosequence. J. Coast. Res. 26 (4), 736–742.

Tanaka, N., Nandasena, N.A.K., Jinadasa, K.B.S.N., Sasaki, Y., Tanimoto, K., Mowjood, M.I.M., 2009. Developing effective vegetation bioshield for tsunami protection. Civ. Eng. Environ. Syst. 26 (2), 163–180.

Thompson, K., 1987. Seeds and seed banks. New Phytologist. 106, 23–34.

Thompson, K., Band, S.R., Hodgson, J.G., 1993. Seed sizeand shape predict persistence in soil. Functional Ecology. 7, 236–241.

Thompson, K., Band, S.R., 1997. Survival of a lowland heath-land seed bank after a 33-year burial. Seed Science Research. 7, 409–411.

Wang, Y.C., Ooi, M.K.J., Ren, G.H., Jiang, D.M., Musa, A., Miao, R.H., et al. 2015. 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. Basic and Applied Ecology. 16 (6), 490–499.

Wang, Y., Alberto, B.C., Jiang, D., Ala, M., Li, X., Zhou, Q., Lin, J., Ren, G., Jia, L., 2016. The role of sexual vs. asexual recruitment of *Artemisia wudanica* in transition zone habitats between inter-dune lowlands and active dunes in Inner Mongolia, China. Solid Earth. 7(2), 621–629.

Wootton, L.S., McGough, A., Bevaart, K., Ondreika, J., Patel, P., 2003. Effectiveness of low-impact management strategies for the removal of C. kobomugi (Asiatic sand sedge) from dune communities within New Jersey's coastal parks. In: Coastal Zone 2003 Conference Prceedings, Baltimore, MD.

Xu, Z., Mason, J.A., Lu, H., 2015. Vegetated dune morphodynamics during recent stabilization of the Mu Us dune field, north-central China. Geomorphology. 228, 486–503.

Yan, Q.L., Liu, Z.M., Zhu, J.J., 2009. Temporal variation of soil seed banks in two different dune systems in northeastern Inner Mongolia, China. Environmental Geology. 58 (3), 615–624.

Yan, S., Liu, Z., 2010. Effects of dune stabilization on plant diversity of interdune wetlands in the northeastern Inner Mongolia, China. Land Degradation & Development. 21 (1), 40–47.

Yassir, I., van der Kamp, J., & Buurman, P. 2010. Secondary succession after fire in Imperata grasslands of East Kalimantan, Indonesia. Agriculture, Ecosystems & Environment. 137, 172–182.

Zhang, J., Zhang, Y., Fan, D., Qin, S., Jia, X., Wu, B., et al. 2015. Effects of sand dune stabilization on the spatial pattern of *Artemisia ordosica* population in Mu Us Desert, Northwest China. Plos One. 10 (6).

Zhang, J., Zhao, H., Zhang, T., Zhao, X., Drake, S., 2005. Community succession along a chronosequence of vegetation restoration on sand dunes in Horqin Sandy Land. Journal of Arid Environments. 62, 555–566.

Zuo, X., Wang, S., Zhao, X., Lian, J., 2014. Scale dependence of plant species richness and vegetation-environment relationship along a gradient of dune stabilization in Horqin Sandy Land, Northern China. Journal of Arid Land. 6 (3), 334–342.

Zuo, X., Zhao, X., Wang, S., Li, Y., Lian, J., Zhou, X., 2012. Influence of dune stabilization on relationship between plant diversity and productivity in Horqin Sand Land, Northern China. Environmental Earth Sciences. 67 (5), 1547–1556.

Zuo, X.A., Zhao, H.L., Zhao, X.Y., Zhang, T.H., Guo, Y.R., Wang, S.K., Drake, S., 2008. Spatial pattern and heterogeneity of soil properties in sand dunes under grazing and restoration in Horqin Sandy Land, Northern China. Soil and Tillage Research. 99, 202–212.

Zuo, X., Zhao, H.L., Zhao, X.Y., Guo, Y.R., Li, Y.L., Luo, Y.Y., 2008. Plant distribution at the mobile dune scale and its relevance to soil properties and topographic features. Environmental Geology. 54, 1111–1120.

Tables

Table 1 One-Way ANOVA of the density and coverage, and other characteristics of above-ground vegetation in the inter-dune lowlands of active dunes (AD) and stabilized dunes (SD). The number of samples was 58 for AD and 36 for SD. Values are mean ± SE.

Table 2 One-Way ANOVA of the density, and other characteristics of soil seed bank in the inter-dune lowlands of active dunes (AD) and stabilized dunes (SD). The number of samples was 58 for AD and 36 for SD. Values are mean ± SE.

Table 3 One-Way ANOVA for soil physicochemical characteristics in the inter-dune lowlands of active dunes (AD) and stabilized dunes (SD). The number of samples was 58 for AD and 36 for SD. Values are mean ± SE.

Table 4 Mean importance values (IV) for all the species in plant communities and soil seed bank in the inter-dune lowlands of active dunes (AD) and stabilized dunes (SD). AH = annual herb, ABH = annual-biennial herb, BH = biennial herb, PH = perennial herb, SS = semi-shrub, S = shrub, T = tree. P = psammophyte, LMS = limnocryptophyte-meadow species, STS = steppe species.

Table 1 One-Way ANOVA of the density and coverage, and other characteristics of above-ground vegetation in the inter-dune lowlands of active dunes (AD) and stabilized dunes (SD). The number of samples was 58 for AD and 36 for SD. Values are mean ± SE.

	Total species richness	coverage (%)	Density (individuals m^{-2})	Simpson diversity index (D)	Shannon-wiener Index (H)	Pielou index (E)
Active dunes (AD)	44	61±5	149±17	0.94	3.20	0.85
Stabilized dunes (SD)	59	89±4	233±36	0.95	3.41	0.84
F		16.28	5.55			
P		0.00	0.02			

Table 2 One-Way ANOVA of the density, and other characteristics of soil seed bank in the inter-dune lowlands of active dunes (AD) and stabilized dunes (SD). The number of samples was 58 for AD and 36 for SD. Values are mean ± SE.

	0-5 cm					5-10 cm					0-10 cm				
	Total species richness	Density (individuals m^{-2})	Simpson diversity index	Shannon-wiener Index	Pielou index	Total species richness	Density (individuals m^{-2})	Simpson diversity index	Shannon-wiener Index	Pielou index	Total species richness	Density (individuals m^{-2})	Simpson diversity index	Shannon-wiener Index	Pielou index
Active dunes (AD)	19	7536±1344	0.81	1.80	0.61	17	4063±739	0.80	1.76	0.62	23	11599±1980	0.81	1.80	0.57
Stabilized dunes (SD)	16	5644±1172	0.49	1.19	0.43	10	1429±463	0.27	0.70	0.30	19	7074±1477	0.45	1.13	0.38
F		0.95					6.83					2.66			
P		0.33					0.01					0.11			

Table 3 One-Way ANOVA for soil physicochemical characteristics in the inter-dune lowlands of active dunes (AD) and stabilized dunes (SD). The number of samples was 58 for AD and 36 for SD. Values are mean ± SE.

	Organic matter (g kg^{-1})	Total nitrogen (g kg^{-1})	Total phosphorus (g kg^{-1})	pH	C/N
Active dunes (AD)	3.42±0.20	0.23±0.01	0.11±0.01	6.80±0.02	9.10±0.24
Stabilized dunes (SD)	11.38±0.64	0.77±0.03	0.22±0.01	7.30±0.02	8.54±0.26
F	199.56	335.87	126.09	219.34	2.36
P	0.00	0.00	0.00	0.00	0.13

Table 4 Mean importance values (IV) for all the species in plant communities and soil seed bank in the inter-dune lowlands of active dunes (AD) and stabilized dunes (SD). AH = annual herb, ABH = annual-biennial herb, BH = biennial herb, PH = perennial herb, SS = semi-shrub, S = shrub, T = tree. P = psammophyte, LMS = limnocryptophyte-meadow species, STS = steppe species.

	Species	Abbreviated code	Life form	Family	Ecological group	Importance values Above-ground vegetation/ Soil seed bank（0-10cm）				Regional significance
						Active dunes (AD)		Stabilized dunes (SD)		
1	*Agriophyllum squarrosum*	*A. squarrosum*	AH	Chenopodiaceae	p	6	0		0	
2	*Setaria viridis*	*S. viridis*	AH	Gramineae	LMS	49	26	60	11	
3	*Corispermum candelabrum*	*C. candelabrum*	AH	Chenopodiaceae	p	26	11		3	
4	*Chenopodium glaucum*	*C. glaucum*	AH	Chenopodiaceae	LMS	25	19	19	73	
5	*Chenopodium glaucum*	*C. glaucum*	AH	Chenopodiaceae	LMS	9	18	7	2	
6	*Abutilon theophrasti Medic*	*A. theophrasti*	AH	Malvaceae	LMS			1		
7	*Glycine soja*	*G. soja*	AH	Leguminosae	LMS	1	0	4	0	
8	*Chenopodium aristatum*	*C. aristatum*	AH	Chenopodiaceae	LMS	10	0	3	1	
9	*Salsola ruthenica*	*S. ruthenica*	AH	Chenopodiaceae	LMS			2		
10	*Eragrostis pilosa*	*E. pilosa*	AH	Gramineae	LMS	2	23	17	0	
11	*Bassia dasyphylla*	*B. dasyphylla*	AH	Chenopodiaceae	STS			1		
12	*Cuscuta chinensis*	*C. chinensis*	AH	convolvulaceae	STS	1				
13	*Digitaria sanguinalis*	*D. sanguinalis*	AH	Gramineae	LMS	8	2	6	2	
14	*Euphorbia humifusa*	*E. humifusa*	AH	Euphorbiaceae	LMS		0	5	0	
15	*Chloris virgata*	*C. virgata*	AH	Gramineae	LMS		0	30	0	
16	*Kochia scoparia*	*K. scoparia*	AH	Chenopodiaceae	LMS			3		
17	*Orobanche coerulescens*	*O. coerulescens*	AH	Orobanchaceae	STS			1		

18	*Xanthium sibiricum*	*X. sibiricum*	AH	Compositae	STS			1	
19	*Tribulus terrestris*	*T. terrestris*	AH	Zygophyllaceae	LMS			6	
20	*Lactuca indica*	*L. indica*	ABH	Compositae	LMS	16		2	
21	*Melilotus suaveolens*	*M. suaveolens*	ABH	Leguminosae	LMS	4	0	9	
22	*Artemisia sieversiana*	*A. sieversiana*	ABH	Compositae	LMS	2	1	13	
23	*Artemisia scoparia*	*A. scoparia*	ABH	Compositae	STS	1		39	
24	*Lappula echinata*	*L. echinata*	ABH	Boraginaceae	STS		1	16	
25	*Erigeron acer*	*E. acer*	BH	Chenopodiaceae	LMS			1	
26	*Phragmites communis*	*P. communis*	PH	Gramineae	P/LMS	25		19	
27	*Calamagrostis epigeios*	*C. epigeios*	PH	Gramineae	LMS	14		2	
28	*Vicia amoena*	*V. amoena*	PH	Leguminosae	LMS	13	0	2	0
29	*Thermopsis lanceolata*	*T. lanceolata*	PH	Leguminosae	LMS	1		6	
30	*Juncellus serotinus*	*J. serotinus*	PH	Cyperaceae	LMS	5	0	8	1
31	*Artemisia sacrorum*	*A. sacrorum*	PH	Compositae	STS	3	0	16	
32	*Artemisia lavandulaefolia*	*A. lavandulaefolia*	PH	Compositae	LMS	4	0	3	
33	*Ixeris chinensis*	*I. chinensis*	PH	Compositae	STS	11		2	
34	*Sonchus brachyotus*	*S. brachyotus*	PH	Compositae	STS	1		2	0
35	*Carex duriuscula*	*C. duriuscula*	PH	Cyperaceae	STS	1	0		1
36	*Inula britannica*	*I. britannica*	PH	Compositae	LMS	1		2	
37	*Cynanchum thesioides*	*C. thesioides*	PH	Asclepiadaceae	STS	11		1	
38	*Silene jenisseensis*	*S. jenisseensis*	PH	Caryophyllaceae	STS			4	
39	*Taraxacum mongolicum*	*T. mongolicum*	PH	Compositae	LMS			2	
40	*Linaria vulgaris*	*L. vulgaris*	PH	Scrophulariaceae	LMS	2			
41	*Pennisetum centrasiaticum*	*P. centrasiaticum*	PH	Gramineae	P/LMS			6	
42	*Medicago ruthenica*	*M. ruthenica*	PH	Leguminosae	STS	3		4	
43	*Scutellaria baicalensis*	*S. baicalensis*	PH	Labiatae	STS	2		4	

44	*Lactuca tatarica*	*L. tatarica*	PH	Compositae	LMS	1				
45	*Equisetum ramosissimum*	*E. ramosissimum*	PH	Equisetaceae	LMS	1		21		
46	*Agrostis clavata*	*A. clavata*	PH	Gramineae	LMS			3		
47	*Triarrherca sacchariflora*	*T. sacchariflora*	PH	Gramineae	LMS	1		1		
48	*Tatarian aster root*	*T. aster*	PH	Compositae	STS	3				
49	*Cleistogenes squarrosa*	*C. squarrosa*	PH	Gramineae	STS			8		
50	*Asparagus cochinchinensis*	*A. cochinchinensis*	PH	Liliaceae	STS			1		
51	*Senecio jacobacea*	*S. jacobacea*	PH	Compositae	STS	4		3	0	
52	*Astragalus adsurgens*	*A. adsurgens*	PH	Leguminosae	LMS	1		8		
53	*Heteropappus altaicus*	*H. altaicus*	PH	Compositae	STS	5				
54	*Leymus chinensis*	*L. chinensis*	PH	Gramineae	STS			13		
55	*Allium odorum*	*A. odorum*	PH	Liliaceae	LMS			4		
56	*Saposhnikovia divaricata*	*S. divaricata*	PH	Umbelliferae	STS			2		
57	*Apocynum venetum*	*A. venetum*	PH	Apocynaceae	STS			2		
58	*Galium verum*	*G. verum*	PH	Rubiaceae	STS			2		
59	*Sanguisorba officinalis*	*S. officinalis*	PH	Rosaceae	STS			2		
60	*Euphorbia esula*	*E. esula*	PH	Euphorbiaceae	STS			1		
61	*Plantago depressa*	*P. depressa*	PH	Plantaginaceae	LMS			2		
62	*Medicago ruthenica*	*M. ruthenica*	PH	Leguminosae	STS			1		
63	*Bolboschoenus compacts*	*B. compacts*	PH	Cyperaceae	LMS		0		2	Rare
64	*Trifolium repens*	*T. repens*	PH	Leguminosae	LMS		0			
65	*Dianthus chinensis*	*D. chinensis*	PH	Caryophyllaceae	STS		0			
66	*Artemisia wudanica*	*A. wudanica*	SS	Compositae	p	3				Endemic
67	*Sophora flavescens*	*S. flavescens*	SS	Leguminosae	p	4		4		Rare
68	*Hedysarum fruticosum*	*H. fruticosum*	SS	Leguminosae	p	22				Rare
69	*Swainsona salsula*	*S. salsula*	SS	Leguminosae	LMS			3		

70	*Lespedeza davurica*	*L. davurica*	SS	Leguminosae	LMS	2		3	3	
71	*Salix gordejevii*	*S. gordejevii*	S	Salicaceae	p	18		2	1	Rare
72	*Salix microstachya*	*S. microstachya*	S	Salicaceae	p	18		33		Rare
73	*Caragana microphylla*	*C. microphylla*	S	Leguminosae	p	5	0			Rare
74	*Populus spp.*	*P. spp.*	T	Salicaceae	LMS	1				

Figure legends

Fig. 1 Species richness and average density of above-ground vegetation (a) and the soil seed bank (b) in the inter-dune lowlands of active dunes (AD) and stabilized dunes (SD) with standard error (SE) bar.

Fig. 2 Detrended Correspondence Analysis (DCA) of species composition between above-ground vegetation and the soil seed bank in the inter-dune lowlands of active dunes (AD) and stabilized dunes (SD).

Fig. 3. Canonical Correlation Analysis (CCA) (a) and Redundancy Analysis (RDA) (b) of the correlation between vegetation, soil seed bank and environmental factors in the inter-dune lowlands of active dunes (AD) and stabilized dunes (SD).

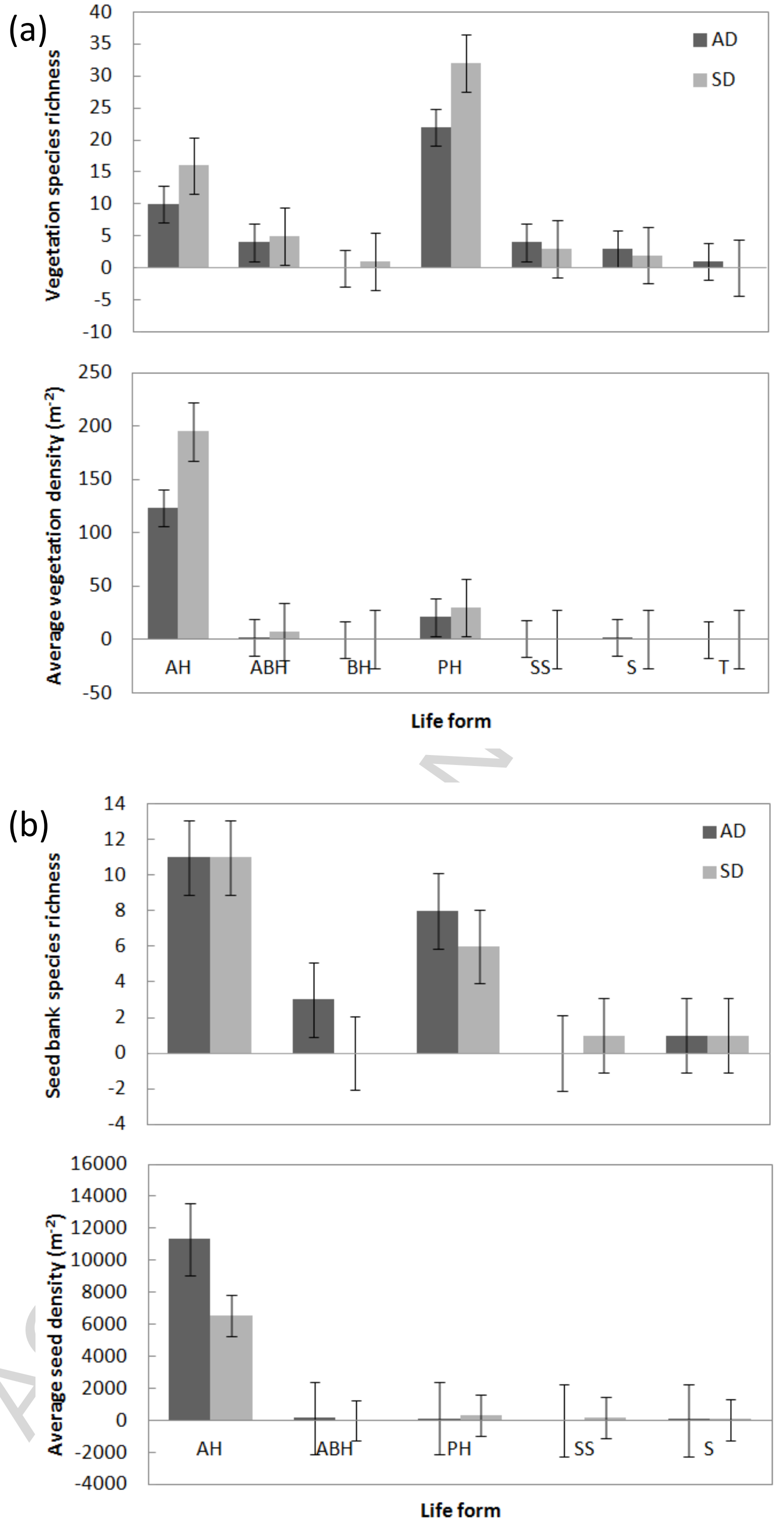


Fig. 1. Species richness and average density of above-ground vegetation (a) and the soil seed bank (b) in the inter-dune lowlands of active dunes (AD) and stabilized dunes (SD) with standard error (SE) bar.

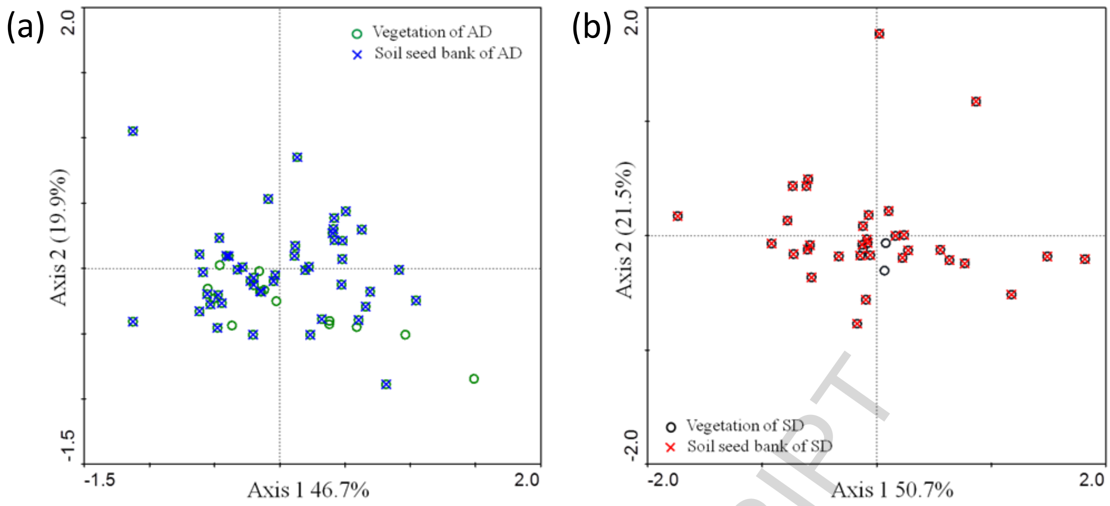


Fig. 2. Detrended Correspondence Analysis (DCA) of species composition between above-ground vegetation and the soil seed bank in the inter-dune lowlands of active dunes (AD) and stabilized dunes (SD).

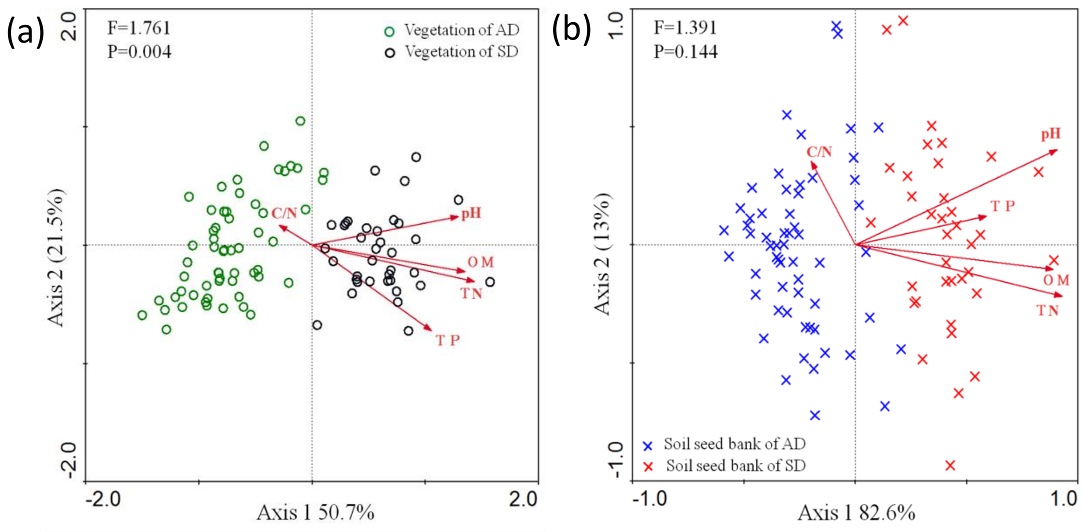
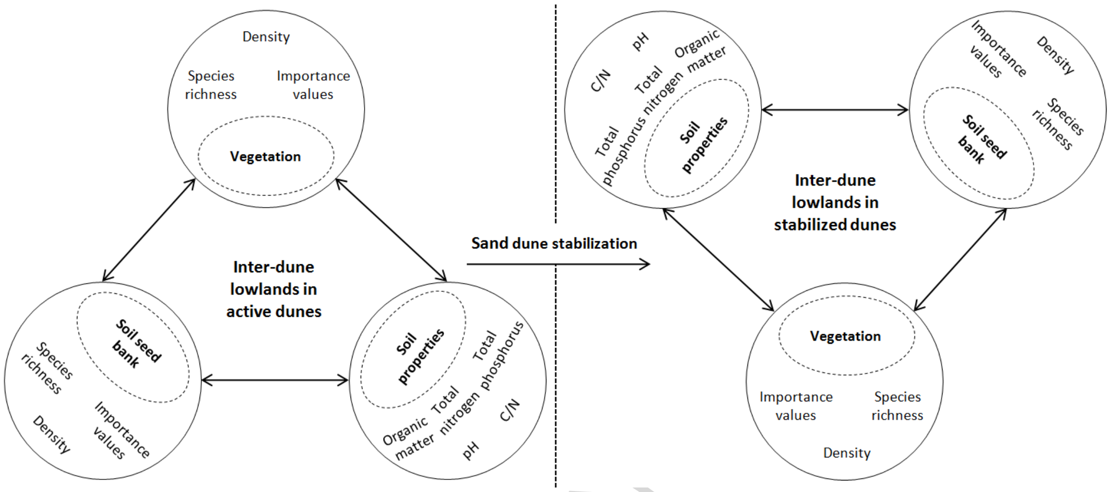


Fig. 3. Canonical Correlation Analysis (CCA) (a) and Redundancy Analysis (RDA) (b) of the correlation between vegetation, soil seed bank and environmental factors in the inter-dune lowlands of active dunes (AD) and stabilized dunes (SD).

Graphical Abstract

This study contributes towards a better understanding of sand dune stabilization by showing the changes in the characteristics of above-ground vegetation and soil seed bank, including their correlations with environmental factors.



Highlights

- Aboveground vegetation species richness increased with sand dune stabilization.
- Soil seed bank species richness declined with sand dune stabilization.
- Inter-dune lowland of active sand dunes is suitable for some endemic species.
- Conservation areas should be set up in active sand dunes to protect biodiversity.