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Structure, pattern and mechanisms of formation of seed banks in sand dune systems in northeastern Inner Mongolia, China

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Abstract

A comparison of structure and pattern of the soil seed bank was made between active and stabilized sand dunes in northeastern Inner Mongolia, China. The objective of this paper was to determine the significance of seed bank in vegetation restoration of sand dunes. The results showed that (1) average seed density decreased from stabilized sand dune to interdune lowland of stabilized sand dune, to interdune lowland of active sand dune, and to active sand dune; (2) horizontally, along the transect from interdune lowland to ecotone and to sand dune top, a 'V' shaped pattern was presented in the active dune system, and a reverse 'V' shaped pattern in the stabilized sand dune system; (3) vertically, the proportion (accounting for the total seeds) of seeds found in 0–20 mm soil profile decreased from stabilized sand dune to interdune lowland of stabilized sand dune, to interdune lowland of active sand dune, and to active sand dune. The same order was also found in 20–50 mm and 50–100 mm soil profiles; (4) the Sokal and Sneath similarity indices in the species-composition between soil seed bank and above-ground vegetation were ranked as: the stabilized sand dune (24%) > the interdune lowland of active sand dune (21%) > the interdune lowland of stabilized sand dune (18%) > the active sand dune (5%); and (5) vegetation restoration of active sand dunes depends on the dispersal of seeds from nearby plant communities on the interdune lowlands. Much effort must be made to preserve the lowlands, as lowlands are the most important seed reservoir in the active sand dune field.

Introduction

Desertification is referred to as land degradation in arid, semi-arid and dry sub-humid areas resulting from various factors, including climatic variations and human activities (Kassas, 1995). Desertification may lead to formation of sand dunes (Zhu and Chen, 1994), and sand mobility and wind erosion are the main characteristics of active sand dunes. Vegetation restoration on sand dune is a major challenge for ecologists, and a great number of studies in this aspect have been conducted (e.g., Lichter, 2000; Yu et al., 2003).

Generally, regeneration strategies of plants are shaped by the patterns of disturbance and stress (Grime, 2001; Grubb, 1977). Seeds in soil, as one regenerative aspect, are often more tolerant of adverse conditions than their adult counterparts, and they may escape from agents of disturbance, disease and predation (Bakker et al., 1996b). In addition, seed populations in soils play prominent ecological and evolutionary roles

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in linking past, present, and future plant population and community structure and dynamics (Leck et al., 1989; Thompson and Grime, 1979). There have been intensive studies on seed banks in many kinds of ecosystems (e.g., Chang et al., 2001; Witkowski and Garner, 2000). Much attention has been paid to the significance of soil seed banks on vegetation restoration (e.g., Bekker et al., 1997; Thompson, 1992).

Soil seed banks are considered to have important impacts on mitigating the risk of species extinction on sand dunes (Wang and Liang, 1995). However, little information is available on the structure, pattern and mechanisms of formation of seed banks in sand dune systems.

The Horqin Steppe, a typical temperate degraded grassland in the agropastoral zone in Inner Mongolia of northern China (118°35′–123°30′E, 42°41′–45°15′N), has suffered from severe desertification, and active sand dunes are well developed (Liu et al., 1996; Zhu and Chen, 1994). The coexistence of active and stabilized sand dunes facilitates the studies on the structure and pattern of seed banks in sand dune systems, especially the study on the comparison between active and stabilized sand dunes.

In this study, we compared the structure and pattern of the soil seed banks in active and stabilized sand dune systems. We hypothesized that: 1) the structure and pattern of the soil seed banks in these two dune systems would be quite different; 2) significant differences in relativity of seed density and species abundance between active and stabilized sand dunes would exist; and 3) strong wind action would play a major role in shaping the distribution pattern of the soil seed bank in active sand dunes.

Materials and methods

Study site

Investigation was conducted at Wulanaodu village (119°39′–120°02′ E, 42°29′–43°06′ N, 480 m a.s.l.) of the Horqin Steppe in northeastern Inner Mongolia (Figure 1). The annual average temperature of the study area is 6.3 with January the coldest month averaging −14.0°C, and July the warmest averaging 23.0. Mean annual precipitation is 340 mm, of which 70% rains in June, July and August. Annual mean wind velocity is 4.4 m s^{-1}, and the number of gale days (> 16m s^{-1}) is 21–80. The main direction of wind is northwestern.

Two types of systems, i.e., active and stabilized sand dune systems, were selected in the study. The active sand dune system (119°36′E, 43°59′N) is composed of three parts: an active sand dune, an interdune lowland, and an ecotone between the active sand dune and the lowland (Figure 2a). The investigated active dune, 25 m in height, and advancing at a rate of 5–7 m yr^{-1}, was located close to the investigated stabilized dune. The vegetation, composed of only a few pioneering plant species such as *Agriophyllum squarrosum* Moq. and *Artemisia wudanica* Liou & W., had a coverage less than 5%. Sand movement, resulting in either accumulation or erosion, is very distinctive. The interdune lowland, about 6.2 ha and surrounded by crescent dunes, had good moisture. It was well vegetated with hygrophilous species, such as *Parnassia palustris* L., *Typha minima* Funk-Hoppe, *Bolboschoenus compacts* Hoffm., *Carex duriuscula* C. A. Mey, *Vicia amoena* Fisch., etc. The ecotone, located at the windward toe of dune, was drier than the

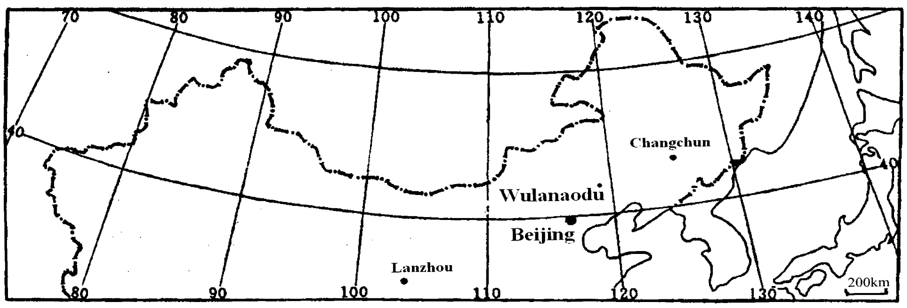

Figure 1. Geographic location of study site (119°39′–120°02′ E, 42°29′–43°06′ N).

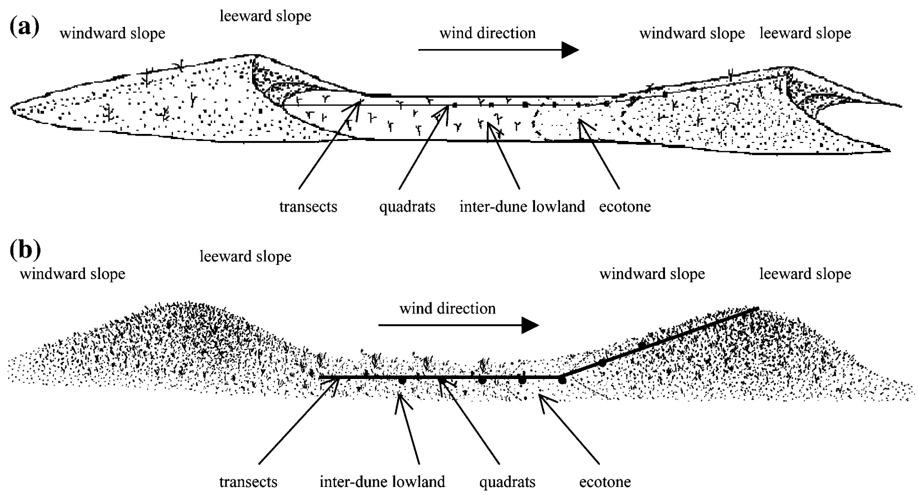

Figure 2. A sketch map of transects and quadrats showing the active sand dune system (a) and the stabilized sand dune system (b).

lowland, and was colonized by pioneering plant species such as *Salix gordejevii* Chang & Skv. and *Phragmites communis* Trin.

The stabilized sand dune system (119°42′ E, 43°52′ N), had an artificially stabilized sand dune, an interdune lowland and an ecotone between the stabilized sand dune and the lowland (Figure 2b). The investigated stabilized dune, which was an active sand dune twenty years ago, was artificially stabilized with both sand barriers and plantation in 1984. Many plant species, such as *Chenopodium glaucum* L., *C. acuminatum* Willd., *Corispermum candelabrum* Iljin, *Bassia dasyphylla* O. Kuntze, *Chloris virgata* Swartz, *Setaria viridis* Beauv., *Digitaria cilliaris* Koel., had encroached naturally, and the vegetation cover was greater than 50%. The interdune lowland, about 4.6 ha, with better moisture condition than the dune, was well vegetated with hygrophilous species of *Eupatorium lindleyanum* DC., *Bolboschoenus compacts* Hoffm., *Carex duriuscula* C. A. Mey, etc. The moisture condition of the ecotone was similar to the lowland.

Methods

Soil seed bank investigation

The investigation of soil seed banks was conducted in early April 2004 (Spring) after seed dispersal and before any germination event (Meissner and Facelli, 1999). Ten transects (northwest direction), each 15 m apart, were run through both sand dune systems. 26 cores were collected at an interval of 15 m along each transect, 13 from the windward slope and 4 from the ecotone, and 9 from the lowland in the active sand dune system (Figure 2a). 10 soil sample cores were collected at an interval of 15 m along each transect, of which 4 soil samples were collected from the windward slope of the sand dune, 2 from the ecotone, and 4 from the lowland in the stabilized sand dune system, respectively (Figure 2b).

Before the sampling year (i.e., 2003), seeds were collected for species identification of the seed banks. Each soil sample was collected using a cylindrical trowel of 70-mm diameter and collected in three soil profiles 0–20, 20–50, and 50–100 mm. Soil seed bank composition was assessed by seed extraction, which is more accurate than the germination method since it estimates both germinable and dormant seeds (Meissner and Facelli, 1999). After air-dried, the soil samples were sieved through a 0.5-mm sieve. Seeds were extracted, and viability was tested (Paker and Venable, 1996). Only viable seeds were considered to study the structure and pattern of soil seed banks

Vegetation investigation

In August 2004, when vegetation was well developed, plant abundance and species composition were investigated. Ten transects (northwest direction), each 15 m apart, were run through each of the two systems. In the active sand dune system, 26 1 m × 1 m quadrats were selected at an interval of 15 m along each transect. Thirteen quadrats were set on the windward slope, 4 on the ecotone, and 9 on the lowland (Figure 2a). In the stabilized sand dune system, 10 1 m × 1 m quadrats were selected at an interval of 15 m along each transect, of which 4 quadrats were set on the windward slope, 2 on the ecotone and 4 on the lowland (Figure 2b). Each quadrat corresponded to a point for soil seed bank sample collection, i.e., in each quadrat, there was a corresponding soil core collected in April.

Data analysis

Differences between seed density in different habitats were analyzed with the Student's *t*-test. We tested for the correlations between soil seed bank and species abundance of the established vegetation using Bivariate Correlations. The critical *P*-values for the Student's *t*-test and for pairwise comparisons among seed density were Bonferroni-corrected. The similarity index in species-composition between soil seed bank and above-ground vegetation was calculated following Sokal and Sneath (1963).

Results

Overall seed bank characteristics of two types of systems

Average seed density decreased from stabilized sand dune to interdune lowland of stabilized sand dune, to interdune lowland of active sand dune, and to active sand dune (Figure 3). There were significant differences in seed density between the active dune and other habitat types, i.e., the lowland of active dune, the stabilized dune, and the lowland of stabilized dune ($P < 0.01$).

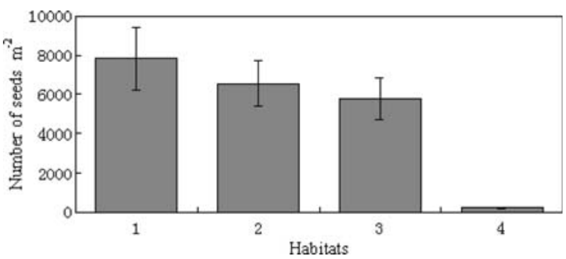

Figure 3. Average seed density of stabilized sand dune (1), interdune lowland of stabilized sand dune (2), interdune lowland of active sand dune (3), and active sand dune (4).

Horizontal distribution of soil seed banks in two types of systems

Seed density pattern differed between active and stabilized sand dune systems. In the active dune system, seed density was the highest in the interdune lowland, and there was a peak of seed density in the middle of lowland. Toward the ecotone, the seed density decreased strikingly, and at the ecotone, the density was nearly zero. From the ecotone to active sand dune top, seed density was slightly increased. Overall, along the transect from interdune lowland to ecotone and to sand dune top, a 'V' shaped pattern of seed density was formed (Figure $4a_1$). On the contrary, in the stabilized sand dune system, there was a low seed density in the middle of lowland initially, then toward the ecotone the density increased strikingly, and at the ecotone there was a peak of seed density. From the ecotone to the dune top, seed density decreased gradually, and a low density was found on the dune top. Therefore, along the transect from interdune lowland to ecotone and to sand dune top, a reverse 'V' shaped pattern of seed density was formed (Figure $4a_2$).

Seed distribution patterns of the individual species were not necessarily consistent with the pattern mentioned above. Three distribution types for each system were classified as follows.

Type I – seeds only occurred in the lowland and in the ecotone. In this type seeds decreased gradually toward the ecotone. In the active sand dune system, *Carex duriuscula* C. A. Mey, *Setaria viridis* Beauv., *Digitaria cilliaris* Koel., *Glycine soja* Sieb. & Zucc. (Figure 4b) and *Erigeron acer* L., *Lespedeza davurica* Schindl., *Cyperus glomeratus* L., *Eragrostis pilosa* Beauv. and *Calamagrostis epigeios* Roth fell into this group. In the stabilized sand dune system, *Glycine soja* Sieb. & Zucc., *Chloris virgata* Swartz (Figure 4c), *Eupatorium lindleyanum* DC., *Erigeron acer* L., *Lespedeza davurica* Schindl. and *Vicia amoena* Fisch. were representative in this group.

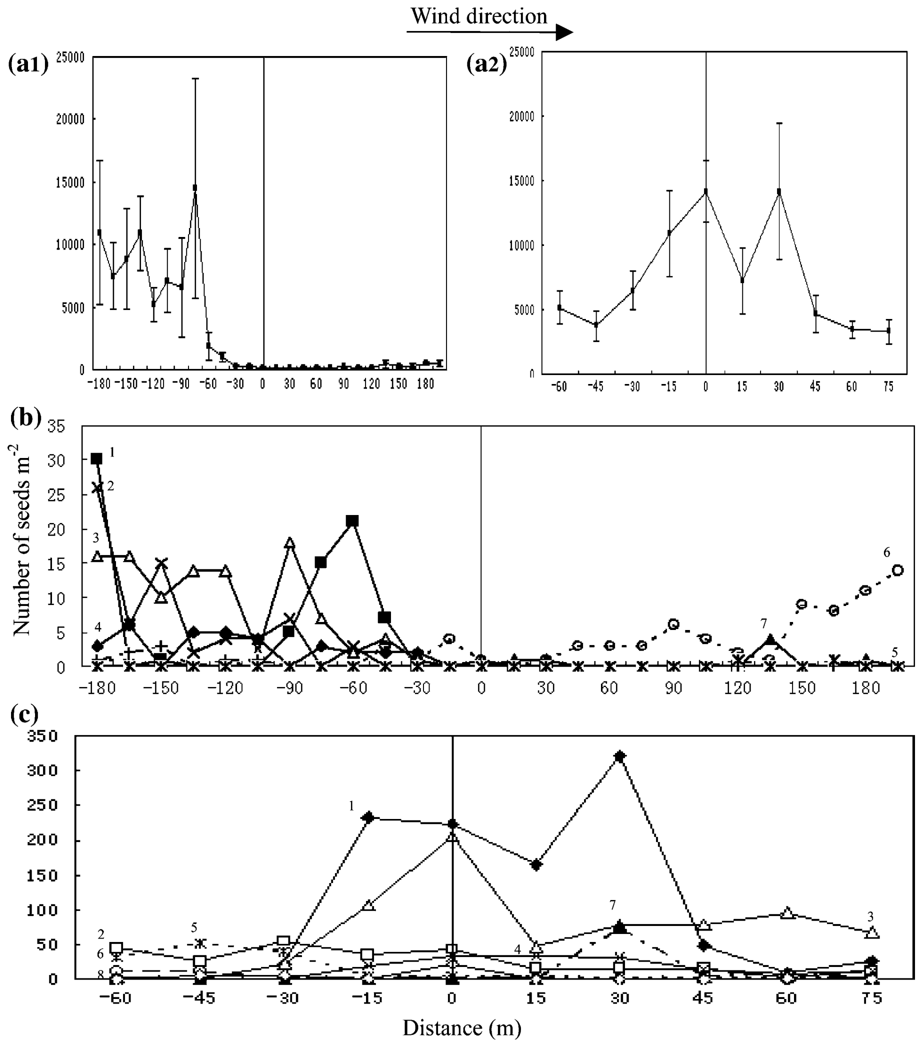

Figure 4. Horizontal distribution of soil seed banks in the active sand dune system (a_1) and in the stabilized sand dune system (a_2). Horizontal distribution of some species in the active sand dune system (b) (1. *Digitaria cilliaris* Koel.; 2. *Glycine soja* Sieb. & Zucc.; 3. *Carex duriuscula* C. A. Mey; 4. *Setaria viridis* Beauv.; 5. *Enneapogon brachystachyus* Stapf; 6. *Agriophyllum squarrosum* Moq.; and 7. *Artemisia wudanica* Liou & W.) and in the stabilized sand dune system (c) (1. *Chenopodium acuminatum* Willd.; 2. *Setaria viridis* Beauv.; 3. *Corispermum candelabrum* Iljin; 4. *Chenopodium glaucum* L.; 5. *Chloris virgata* Swartz; 6. *Glycine soja* Sieb. & Zucc.; 7. *Bassia dasyphylla* O. Kuntze; and 8. *Eragrostis pilosa* Beauv.). Zero (m) is the central point of the ecotone of each system. Interdune lowland is at the left of zero, and sand dune is at right.

Type II – seeds were presented only in the sand dune. In this group, a great number of seeds occurred in the middle of windward slope. *Artemisia wudanica* Liou & W. and *Enneapogon brachystachyus* Stapf (Figure 4b), and *Bassia dasyphylla* O. Kuntze (Figure 4c), were included in this category.

Type III – seeds were found in the lowland, in the ecotone and in the dune. In the active sand dune system, there were a great number of *Chloris virgata* Swartz seeds in the middle of lowland, few at the ecotone and a few in the sand dune. The distribution of *Agriophyllum squarrosum* Moq. seeds was much different from that of *Chloris virgata* Swartz, i.e., seed density increased gradually from the lowland to the dune top, and there were three sections where seed density was high: the ecotone, the middle of windward slope and the dune top (Figure 4b). In the stabilized sand dune system, five species belonged to group III, but different distribution patterns of soil seed bank could be found. The distribution pattern of *Chenopodium acuminatum* Willd. was closely similar to the reverse 'V' shaped pattern. *Corispermum candelabrum* Iljin and *Chenopodium glaucum* L. presented a seed peak at the ecotone. Along the transect from lowland to sand dune, the seed density of *Setaria viridis* Beauv. and *Eragrostis pilosa* Beauv. were nearly unchanged (Figure 4c).

Vertical distribution of soil seed banks in two types of systems

Generally, a decline trend in seed bank size from the upper to the deeper soil profiles could be found in the two types of systems. There were significant differences between active and stabilized sand dune systems in the soil profiles of 0–20, 20–50 and 50–100 mm ($P < 0.01$). The proportion (accounting for the total seeds) of seeds found in 0–20 mm soil profile decreased from stabilized sand dune to interdune lowland of stabilized sand dune, to interdune lowland of active sand dune, and to active sand dune. The same order was also found in 20–50 and 50–100 mm soil profiles (Figure 5).

Similar to horizontal distributions, species differed in their vertical distributions. In the active sand dune, most of the seeds of *Agriophyllum squarrosum* Moq. and *Enneapogon brachystachyus* Stapf were on the soil surface, whereas more than half of the seeds of *Chloris virgata* Swartz were found below 20 mm soil profile. Seeds of *Artemisia wudanica* Liou & W. only occurred in the 0–20 and 50–100 mm soil profiles (Figure 6). In the stabilized sand dune, the vertical distributions of all species decreased from the upper to the deeper soil profiles.

Relationship between vegetation and soil seed bank

Horizontally, there was a negative correlation between soil seed bank and species abundance of the established vegetation in the stabilized sand dune and in its lowland. On the contrary, there was a positive correlation in the active sand dune and in its lowland ($P < 0.001$). Seed density of *Agriophyllum squarrosum* Moq. in the active sand dune was significantly correlated with plant abundance of this species ($P < 0.05$) (Figure 7). Correlations between seed density and plant abundance of the 4 species included in stabilized sand dune were not significant (Figure 7).

Vertically, in active sand dune (lowland and ecotone excluded), total plant abundance was significantly correlated with seed density in the 0–20 mm, 20–50 mm and 50–100 mm soil profiles (correlation coefficients were −0.85, −0.78 and −0.60, respectively, $P < 0.01$). There was no significant correlation in the stabilized sand dune (lowland and ecotone excluded).

There was no close correspondence between species-composition in the seed reservoir and species-composition in the established vegetation at

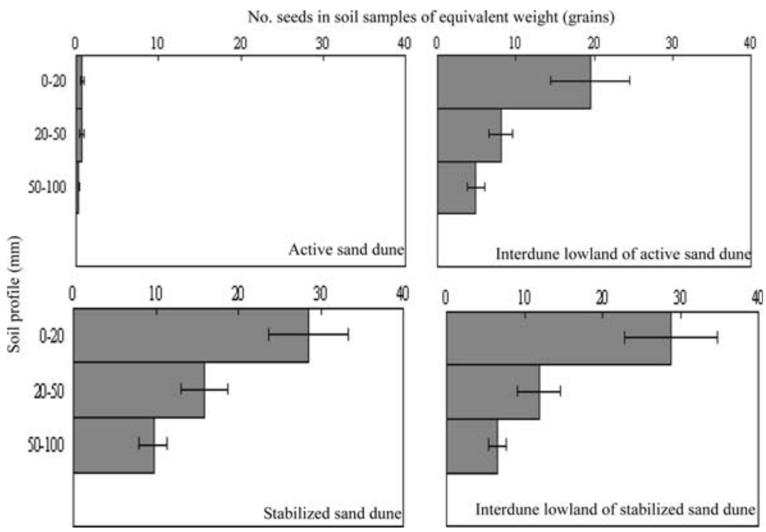

Figure 5. Vertical distribution of total seed populations at the three soil profile categories in soil samples of equivalent weight.

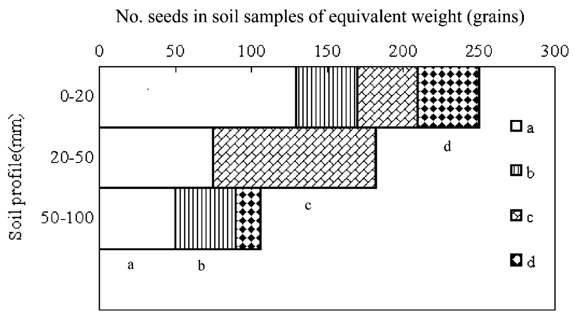

Figure 6. Vertical distribution of 4 species included in active sand dune in soil samples of equivalent weight. a = *Agriophyllum squarrosum* Moq.; b = *Artemisia wudanica* Liou & W.; c = *Chloris virgata* Swartz; d = *Enneapogon brachystachyus* Stapf.

any of the four habitat types, i.e., the stabilized sand dune, the interdune lowland of active sand dune, the interdune lowland of stabilized sand dune and the active sand dune. The Sokal and Sneath similarity indices in the species-composition between soil seed bank and above-ground vegetation were ranked as: the stabilized sand dune (24%) > the interdune lowland of active sand dune (21%) > the interdune lowland of stabilized sand dune (18%) > the active sand dune (5%).

Discussion

Mechanisms of formation of seed distribution patterns

The presence of seeds in disturbed habitats is determined by the relationships between the original plant assemblages, propagule production and seed reserves in the soil (Grime, 2001). Abiotic factors affecting the temporal and spatial patterns of seed bank include wind regime, landform, soil condition, etc. (Chambers and MacMahon, 1994; Chambers et al., 1991; Okubo and Levin, 1989; Reichman, 1984; Thompson and Grime, 1979), whereas biotic factors include seed shape, seed size, behavior of seed-eating animals, grazing, etc. (Guo et al., 2000; Liddle et al., 1987; Moles et al., 2000; O'Connor and Pickett, 1992; Thompson et al., 1993). Horizontally, both abiotic and biotic factors controlled the seed bank distribution in the active and stabilized sand dune systems, thus making the seed distribution pattern presenting a 'V' shaped one (Figure $4a_1$) and a reverse 'V' shaped one (Figure $4a_2$), respectively.

In the active sand dune system, the most important abiotic factors controlling horizontal seed distribution may be wind action and sand movement. Biotic factors, i.e., canopy seed bank, myxospermy (an anchorage mechanism, where mucilage is produced upon being moistened), seed shape and size are also closely related to dispersal, and therefore related to horizontal seed distribution (van Rheede van oudtshoorn and van Rooyen, 1999; Weiher et al., 1999). Generally, for an active sand dune, the lower part of the windward slope (including the ecotone between interdune lowland and dune body) is the erosion-prone zone, and the upper part of the windward slope (including dune crest) is the burial-prone zone (Zhu, 1963). Under the impact of wind action and sand movement, seeds in soil are redistributed, i.e., seeds located originally in the ecotone as well as in the interdune lowland are blown away and buried in the upper part of the windward slope or dune crest (even in the leeward slope). The investigated lowland was surrounded by crescent-shaped dunes, and by vegetation that was well developed. Due to its optimal landform and wind breaking effect of dense vegetation, interdune lowland has abundant reserves of seeds. Hardly any seeds occurred at the ecotone due to serious wind erosion. Owing to the accumulation of seeds carried by wind, there were more seeds in the upper part of the windward slope than those in the ecotone.

Horizontal distributions of the seeds of *Agriophyllum squarrosum* Moq. and *Artemisia wudanica* Liou & W. contribute much to the overall horizontal distribution pattern in the active sand dune system, and their seed distribution patterns are related to some unique reproductive strategies. Seeds of *A. wudanica* Liou & W. secrete mucilage from achenes upon being moistened and thus adhere to sand grains (Liu et al., 2004; Yan et al., 2004), which would make them too heavy to be blown very far, staying near the parent plants and waiting for favorable conditions (especially rainfall) to germinate. The diaspore of *Agriophyllum squarrosum* Moq. is disc-shaped, thus it is not likely to be carried away by wind (Yan et al., 2004). Furthermore, *A. squarrosum* Moq. has a canopy seed bank (unpublished data), and seed storage in canopy

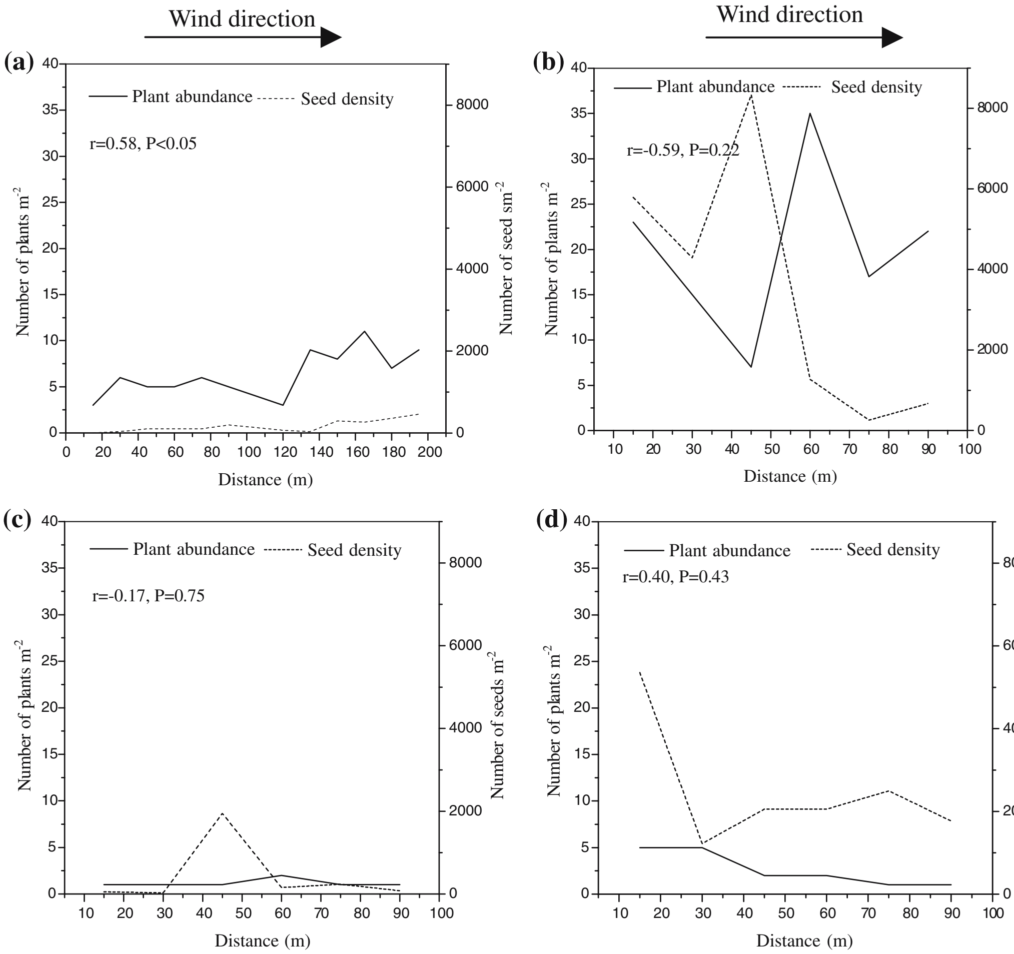

Figure 7. Correlation between plant abundance and horizontal seed density. *R* is the correlation coefficient between plant abundance and seed density of 4 species. a = *Agriophyllum squarrosum* Moq.; b = *Chenopodium acuminatum* Willd.; c = *Bassia dasyphylla* O. Kuntze; d = *Corispermum candelabrum* Iljin. *Agriophyllum squarrosum* Moq. occurred in the active sand dune (lowland and ecotone excluded); and *Chenopodium acuminatum* Willd., *Bassia dasyphylla* O. Kuntze, and *Corispermum candelabrum* Iljin. occurred in the stabilized sand dune (lowland and ecotone excluded). Direction from the windward toe of dunes to the dune top and the wind direction are the same.

in arid zones functions to spread the risk of the offspring encountering unfavorable conditions over a long time (Gutterman and Ginott, 1994; van Rheede van oudtshoorn and van Rooyen, 1999). It is easily concluded that biologic characteristics of plant species (i.e., canopy seed bank, myxospermy, seed morphology) are closely related to the dispersal, controlling the horizontal distribution of soil seed banks.

In the stabilized sand dune system, life form of plant species may play a major role in controlling the horizontal distribution pattern of seed bank. In the initial stage after stabilization, soil (i.e., windblown sand) is loose and mobile, which does not favor species establishment. Annual species are best adapted to the persistent and intense disturbance (Grime, 2001; Weiher et al., 1999), and thus they colonize the dunes as pioneering species. Due to their strong reproductive ability (maybe also to delay in seed release), annual plant species regenerate in huge numbers, and a lot of seeds are produced and buried in the soil. Our investigation showed that about 95% of seeds (7431 ± 1531 seeds m^{-2}) in the soil seed bank of stabilized sand dune were seeds of annuals, and the remaining 5% (391 ± 81 seeds m^{-2}) in the soil seed bank were perennials. It is noticeable that there were a great number of seeds in the ecotone. Good soil moisture and dense vegetation may be responsible for this.

Vertically, total number of seeds declined as soil profile increased in the two types of systems (Figure 5). The vertical distribution pattern for seed density is the same as that obtained from a desert (Guo et al., 1998). Soil condition and behavior of seed-eating animals control the vertical distribution pattern of seed bank (Guo et al., 1998).

Soil seed bank patterns and sand dune restoration

The availability of seeds may be a bottle-neck for re-establishment of plant species after disturbance (Bakker et al., 1996a, b, 2000). The relationship between aboveground vegetation and species in soil seed banks is classified into three types: type I, seeds and their adult counterparts coexist; type II, there are only seeds, no corresponding plants; type III, there are only plants, no seeds (Whipple, 1978).

In this study, we found poor similarity in species composition between seed bank and aboveground vegetation, ranging from 5 to 24%, which shows that the regeneration potential out of soil seed banks of sand dunes is very limited, especially the active sand dunes, and soil seed bank composition is not particularly relevant to explain above-ground plant community composition. Restoration of sand dunes depends on the dispersal of seeds from nearby plant communities.

We found that most seeds existed in the interdune lowland of the active dune system in the interdune lowland and in the ecotone of the stabilized dune system, meaning that the interdune lowland and the ecotone were the important seed reservoirs. The vegetation restoration of active sand dunes can be realized through the dispersing, depositing and accumulating of seeds from these reservoirs and developing of vegetation. However, depositing and accumulating of the seeds in the active sand dunes are restricted greatly by the strong wind action and sand movement. By applying various sand barriers and plantation, the wind action and sand movement can be effectively controlled, and the seeds can be accumulated easily in the active sand dunes. Thus, the former active sand dune would become the stabilized sand dune. Our study has shown that species of stabilized sand dunes are found in the interdune lowland and in the ecotone. For the sake of vegetation restoration, we can modify the horizontal distribution pattern along the transect from interdune lowland to ecotone and to sand dune by adopting some artificial measures to hasten the re-vegetation of the active sand dunes. For example, we can construct sand barriers with tree branches or hay in the windward slope of active sand dunes to keep seeds from being blown away from the windward interdune lowland.

Comparative studies on the structure and pattern of the soil seed bank across two types of sand dune systems in the northeastern Inner Mongolia of China may provide some new insights into the mechanisms of formation of seed distribution patterns and into restoration strategies.

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