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Arrival vs. retention of seeds in bare patches in the semi-arid desertified grassland of Inner Mongolia, northeastern China

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ABSTRACT

Seed availability is critical for vegetation restoration of bare patches in desertified grassland. Many studies explain seed availability by seed arrival or retention, however, no conclusions are universally applicable. Eleven bare patches, ranging from 80 m^2 to 500 m^2, were selected in semi-arid desertified grassland of Inner Mongolia in northeastern China to determine the retained seed:arrived seed ratio and factors (in both seed morphology and patch characteristics) regulating the ratio. From May to August (the germination season), the arrived seeds were more than 208 (grains m^{-2}); the retained ones were less than 93 (grains m^{-2}). From September to November (part of the non-germination season), the arrived or retained seeds were nearly equal to those during May to August ($P > 0.05$). The retained seed:arrived seed ratio was generally less than 20% each season. Seed shape and appendage as well as vegetation cover of bare patches explained 64% of seed retention, but seed mass and patch size explained little. Our study indicated that bare patches in the desertified grassland lacked seeds because of low seed retention and arrival of seed at inopportune times.

1. Introduction

Desertification is one of the most important environmental issues in the world (Kassas, 1995). There are 916,800 km^2 grasslands in the semi-arid region of China; of these grasslands, 90% have degraded (Wang et al., 2008). Desertification leads to formation of sandy bare patches in the degraded grassland. Vegetation restoration at bare patches can reverse environmental deterioration in the grassland, and a great number of studies have been conducted to understand how vegetation is recovered in the desertified grassland (Fernandez et al., 2002; Kalamees and Zobel, 2002; King, 2007; Klausmeier, 1999).

Seed availability is important for vegetation restoration in bare patches of desertified grassland. Seeds from the surrounding patches with dense vegetation can disperse to bare patches. However, in the windy environment, seeds that arrive at bare patches are very likely to be blown away. Therefore, only retained seeds in the bare patches are beneficial to vegetation restoration.

Low seed availability can be caused by (1) low seed dispersal to the patch, (2) low seed capture at the patch, or (3) both. Determining the causes of low seed availability and addressing the relative role of seed dispersal and seed retention in seed availability are very helpful for understanding the mechanism of vegetation restoration of the bare patch. As for seed limitation of sandy bare patches in the desertified grassland of semi-arid region little information is available. Seed rain or seed bank is usually used to assess seed availability (Arrieta and Suárez, 2005; Jakobsson et al., 2006). However, seed availability might be overestimated by using seed rain. Seed bank is good for expressing seed availability, but it fails to tell the cause of small seed bank, i.e., due to low seed arrival or low seed capture (Aguiar and Sala, 1997; Emmerson et al., 2010). Therefore, determining the relationship between seed arrival and seed capture is important for explaining seed availability and planning approaches to vegetation restoration in sandy bare patches of the degraded grassland.

Seed arrival and capture are closely linked to patch characteristics, seed morphology and wind (Augspurger and Franson, 1987; Chambers and Macmahon, 1994). Seed arrival initially is influenced by the size and shape of bare patches (Kotanen, 1997). Since a large proportion of the small patch is close to its edge (Panetta and Wardle, 1992), seeds rapidly disperse to its center. Similarly, for a given area, seeds disperse less to circular patches than to the patches with other shapes because circular patches have the maximal proportion of surface distant from any edge (Miller, 1982). Seed retention is influenced by vegetation cover and bare patch

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size. Seed retention increases with the increase in vegetation cover (Aguiar and Sala, 1997; Dreber and Esler, 2011). Presumably, seed retention decreases with the increase in patch size. In large bare patches, surrounding plants provide less protection from the wind, so seed removal by wind might be more likely. Seed arrival and retention both can be influenced by wind. Seed arrival might be greater at the leeward of the prevailing wind direction than that of other wind directions and seed retention might be opposite.

The importance of bare patch characteristics to seed arrival or capture may depend on seed morphology. Seed mass, shape or appendages all play important roles in dispersal and anchorage (Augspurger and Franson, 1987). Seed mass and shape have been used to predict seed dispersal and retention (Chambers et al., 1991; Debain et al., 2003; Greene and Johnson, 1993). Seed appendage, plumes, wings or thorns, can facilitate or hamper seed anchorage (Chang et al., 2008). Seeds with good dispersal ability may be less sensitive to patch size and shape than those with poor dispersal ability (Kotanen, 1997), and seeds with good anchorage ability may be less sensitive to patch size and vegetation cover than those with poor anchorage ability (Fernandez et al., 2002). In sandy bare patches, however, how seed morphology and patch characteristics regulate seed arrival and retention still remains unknown.

The Horqin Steppe (118°35′–120°30′E, 42°41′–45°15′N), a typical degraded grassland in Inner Mongolia of northeastern China, has a large proportion of bare-sand area. Newly created bare patches are small, but can expand to sand dunes after a long period of time (Zhao et al., 2002). How vegetation is recovered in the dune area has been explored in recent years (Liu et al., 2012; Yan et al., 2007). However, how vegetation processes are linked to the vegetation restoration in the bare sandy patch remains unexplored. Although some studies on seed rain and seed bank of sand dunes in the region have been performed (Ma and Liu, 2008; Yan et al., 2009), the contribution of seed rain to seed availability and the reason for low seed bank are still unclear. Indeed, studies on the retained seed:arrived seed ratio in the bare patch have been conducted in the grassland (Aguiar and Sala, 1997; Jakobsson et al., 2006). But they are concerned about the undegraded grassland and the patch diameter is less than 1 m. Obviously, those results cannot be extrapolated to the sandy bare patches of the desertified grassland where soil has turned to sand and wind erosion is very serious. In addition, when the patch diameter is greater than 10 m, seed dispersal is very likely to be scale-dependent (Munzbergova, 2004).

Previous studies tend to consider seed bank as the seeds captured in the patch (Aguiar and Sala, 1997; Jakobsson et al., 2006). However, seed capture may be overestimated by using seed bank when the original seeds in the surface soil are not excluded.

We studied the retained seed:arrived seed ratio in the bare patch of the Horqin Steppe with regard to patch size, time, and species. Arrived and retained seeds were investigated. To insure that the original seeds in the soil were excluded, paired traps were set. To find out whether the retained seed:arrived seed ratio was scale-dependent, eleven bare patches with areas ranging from 80 m^2 to 500 m^2 were selected. Investigation was carried out every month from May to November to test whether the ratio was changed with time. Plant life form and ecological group were discriminated to know how the ratio was linked to different plant species types. Seed mass, shape, appendage and dispersal agent were employed to test how seed attributes were associated with seed retention; and patch area and vegetation cover were measured to investigate how patch attributes affected seed retention. To test the hypothesis that low seed retention rather than low seed arrival accounts for low seed availability of bare sandy patches in the desertified grassland, we determined the retained seed:arrived seed ratio of different patch sizes, months and species, and analyzed the major factors regulating the ratio.

2. Materials and methods

2.1. Study site

Our study was conducted at Wulanaodu (119°39′–120°02′E, 42°29′–43°06′N, 480 m a.s.l.) of the Horqin Steppe in northeast Inner Mongolia, China. The region has a semi-arid climate. Mean annual temperature is 6.3 °C with months averaging −14 °C in January and 23 °C in July. The annual average precipitation is 340 mm, with 70% of it falling during June to August. Mean wind velocity is 4.4 m s^{-1}, mostly from the northwest, and the number of gale day (>16 m s^{-1}) is 21–80. The windy season is from March to May, and the germination season begins in late April and ends in late August.

Over 90% of the land in the region has been or is being threatened with desertification and bare sandy patches are frequently found in semi-arid grassland (Li et al., 2000). As the grassland has been overgrazed, vegetation cover and individual plant size have decreased and small bare patches have appeared. The bare patches increase and enlarge rapidly, and at last become large ones through mutual connecting. The average radius of newly created bare patches is less than 5 m in the degraded grassland, and it can expand to more than 10 m due to wind erosion (Zhao et al., 2002). The vegetation of bare patches mainly consists of two species *Agriophyllum squarrosum* and *Setaria viridis*, with the coverage less than 10%. Bare patches are surrounded by species-rich areas with vegetation coverage greater than 50%. The vegetation of these areas is mainly composed of steppe species and psammophyte species.

2.2. Bare patch selection and survey

A plot of 1-ha was selected in fenced grassland with gentle topography in the early April of 2010. Eleven bare patches, ranging from 80 m^2 to 500 m^2, with the radius ranging from 5 m to 13 m, were randomly selected within the plot. Each bare patch was an independent unit. The patch shape was close to ellipse or rectangle extending in the direction of the prevailing wind. The vegetation coverage of the bare patches was less than 3%, mainly composed of *A. squarrosum* dead plants in the early April.

Patch area was measured by GPS in the late April 2010 (Table 1). We re-estimated the vegetation cover in August of 2010, when vegetation was well developed.

2.3. Investigation of seed arrival and retention

The germination season is the determinant time for revegetation of bare patches in the semi-arid grassland. Since the germination season begins in the late April and ends in the late August in the study area, we monitored the seed arrival and retention from May to August. To compare the difference in seed arrival and retention between the germination season and the non-germination season, the period from September to November was taken into consideration. The monitoring was not conducted from December to next April, because it is hard to set seed traps in the freezing months. Since most seeds disperse during September and October in the local flora (Liu, 2010), the seed arrival and retention from September to November can be used to partially represent those of the non-germination season.

In each bare patch, transects in eight directions (N, S, E, W, NW, SE, NE, SW) were run from the center to the edge, and paired seed traps, very close between each other, were set along each transect, with an interval of 1 m (Fig. 1). Seed traps (17 cm high and 11 cm in

Table 1
General description of the investigated bare patches.

Bare patch	Location		Altitude (m)	Area (m^2)	Cover	No. of trap-1
	N	E				
1	43°03.523′	119°38.480′	480	483	6%	79
2	43°03.541′	119°38.512′	478	330	8%	66
3	43°03.522′	119°38.548′	477	235	6%	54
4	43°03.601′	119°38.462′	476	209	8%	56
5	43°03.536′	119°38.366′	481	193	7%	47
6	43°03.523′	119°38.414′	480	160	7%	48
7	43°03.565′	119°38.229′	478	140	3%	41
8	43°03.567′	119°38.401′	476	133	7%	45
9	43°03.571′	119°38.363′	479	123	3%	42
10	43°03.571′	119°38.344′	480	105	6%	39
11	43°03.567′	119°38.288′	476	88	9%	37

diameter), with small holes in the bottom for free water drainage, were placed with their rim at ground level. Trap-1 was used to survey the arrived seeds (seeds dispersed to bare patches), and trap-2, filled with seed-removed sand collected from bare patches, was used to estimate the retained seeds (seeds retained in the soil). There were 1106 seed traps in total, in which there were 553 trap-1s and 553 trap-2s. To avoid trap-1s being filled with sand and consequently our misestimating captured seeds, arrived seeds were investigated every half-month from May (before new seed formation) to November (after seed maturation) in 2010. Retained seeds were investigated at the end of May, August and November. We gathered the materials captured by the traps. After the sample was air-dried, seeds were extracted through a 0.5-mm sieve and collected for species identification. The seeds found in canopy sections in traps were also counted. Seed viability was tested following Günster (1994).

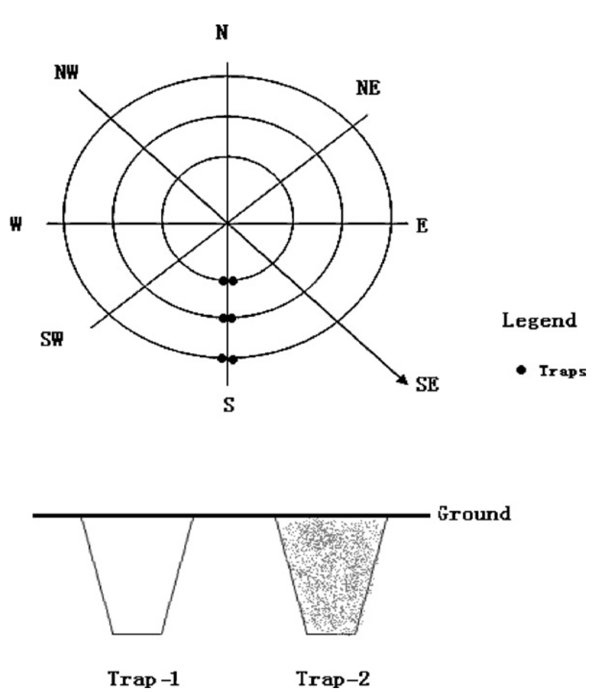

Fig. 1. The graph describing trap setting. Trap-1 was used to survey the arrived seeds (seeds dispersed to bare patches), and trap-2 was used to estimate the retained seeds (seeds retained in the soil). Once seeds fall in the trap-1s, they are protected from removal by wind. The trap-2s, filled with seed-removed sand collected from bare patches, present a surface similar to the surrounding surface, and seeds that land in these traps are not protected from removal by wind.

2.4. Data analyses

Species functional groups were determined following TCSIMNAR (1985), and psammophytes, steppe species and meadow species were classified.

To distinguish the difference of the arrived or retained seeds between time (season), life form and ecological group, the data were analyzed with paired-samples *t*-test. Differences in arrived or retained seeds in eight directions were analyzed with one-way ANOVA analysis. After one-way ANOVA analysis was done, Turkey's test was applied post hoc (SPSS Software, 16th edition) to distinguish the difference in the mean seed number between eight directions. Difference at a level of $P < 0.05$ was considered significant.

The difference between the arrived and the retained seeds was defined as the removed seeds here. Only patch size and vegetation coverage were compared as patch attributes because of similarity of the patch shape. Variations of the removed seeds corresponding to area and vegetation coverage of bare patches were analyzed with Canonical Correspondence Analysis (CCA) using CANOCO 4.

The shape of seeds was determined by the variance of three-dimensions (1ength, width, height); such that when the shape variance was smaller, the seeds were closer to sphericity. Seed mass, seed shape variance and seed appendage were taken from Liu et al. (2003, 2004). We defined: 'with appendage' = 1, and 'without appendage' = 0. Also, variations of the removed seeds corresponding to mass, shape, and appendage of seeds were analyzed with CCA.

3. Results

3.1. The arrived seeds, the retained seeds, and the ratio of retained seed:arrived seed

From May to August (the germination season), the arrived seeds were from 215 to 743 (grains m^{-2}) in different bare patches; the retained ones were from 17 to 93 (grains m^{-2}). The retained seed:arrived seed ratio was less than 20%, ranging from 6% to 16% (Table 2). No evident difference in the arrived or retained seeds in eight directions was found.

From September to November (part of the non-germination season), the arrived seeds were from 129 to 638 (grains m^{-2}) in different bare patches; the retained ones were from 15 to 83 (grains m^{-2}). The ratio was less than 20% in most cases, from 4% to 35% (Table 2). No evident difference in the arrived or retained seeds in eight directions was found. There was no significant difference in arrived or retained seeds between two seasons (Table 2).

Table 2
Arrived and retained seeds (grains m^{-2}) during different periods. R: retained seeds, D: arrived seeds. Seed number is expressed as mean ± SE.

	May–August			September–November			Total		
	R	D	Ratio	R	D	Ratio	R	D	Ratio
1	34 ± 8a	246 ± 36c	14%	56 ± 12a	472 ± 73d	12%	90 ± 15	718 ± 77	13%
2	44 ± 11a	686 ± 69c	6%	26 ± 10a	638 ± 89c	4%	70 ± 15	1324 ± 139	5%
3	52 ± 13a	644 ± 70c	8%	26 ± 11a	196 ± 62d	13%	78 ± 17	841 ± 99	9%
4	93 ± 18a	580 ± 47c	16%	75 ± 20a	425 ± 60c	18%	168 ± 25	1005 ± 78	17%
5	54 ± 13a	479 ± 35c	11%	46 ± 20a	129 ± 22d	35%	100 ± 26	608 ± 38	16%
6	53 ± 14a	743 ± 77c	7%	83 ± 22a	234 ± 67d	35%	136 ± 24	977 ± 95	14%
7	17 ± 6a	215 ± 57c	8%	22 ± 10a	339 ± 53c	6%	39 ± 10	554 ± 93	7%
8	58 ± 19a	420 ± 59c	14%	56 ± 16a	571 ± 100c	10%	113 ± 25	991 ± 114	11%
9	48 ± 11a	450 ± 41c	11%	26 ± 15a	136 ± 31d	19%	74 ± 18	586 ± 49	13%
10	38 ± 9a	267 ± 47c	14%	15 ± 8a	149 ± 29c	10%	54 ± 11	415 ± 61	13%
11	89 ± 15a	564 ± 81c	16%	31 ± 20b	456 ± 79c	7%	119 ± 23	1019 ± 118	12%

Values within a row sharing different letters indicate significant differences in arrived or retained seeds between two seasons ($P < 0.05$).

Table 3
Arrived and retained seeds (grains m^{-2}) of different life forms. R: retained seeds, D: arrived seeds. Seed number is expressed as mean ± SE.

Bare patch	May–August						September–November					
	Annuals			Perennials			Annuals			Perennials		
	R	D	Ratio	R	D	Ratio	R	D	Ratio	R	D	Ratio
1	34 ± 8a	208 ± 21c	16%	0b	38 ± 30d	0	56 ± 12a	470 ± 72c	12%	0b	3 ± 2d	0
2	30 ± 9a	548 ± 63c	5%	14 ± 5b	138 ± 30d	10%	26 ± 10a	629 ± 89c	4%	0b	9 ± 4d	0
3	48 ± 12a	294 ± 46c	16%	4 ± 3b	350 ± 59c	1%	26 ± 11a	154 ± 55c	17%	0b	43 ± 32d	0
4	88 ± 17a	501 ± 43c	18%	5 ± 3b	79 ± 20d	6%	75 ± 20a	420 ± 60c	18%	0b	5 ± 3d	0
5	54 ± 14a	450 ± 35c	12%	0b	29 ± 11d	0	46 ± 20a	125 ± 22c	37%	0b	4 ± 4d	0
6	53 ± 14a	702 ± 72c	8%	0b	40 ± 12d	0	81 ± 21a	234 ± 67c	35%	2 ± 2b	0d	
7	17 ± 6a	210 ± 57c	8%	0b	5 ± 3d	0	22 ± 10a	334 ± 53c	7%	0b	5 ± 3d	0
8	58 ± 16a	411 ± 59c	14%	0b	9 ± 4d	0	56 ± 16a	571 ± 101c	10%	0b	0d	
9	48 ± 11a	262 ± 39c	18%	0b	26 ± 11d	0	26 ± 15a	131 ± 31c	20%	0b	5 ± 3d	0
10	38 ± 9a	267 ± 47c	14%	0b	0d		15 ± 8a	149 ± 29c	10%	0b	0d	
11	89 ± 15a	547 ± 82c	16%	0b	17 ± 6d	0	31 ± 20a	450 ± 80c	7%	0b	6 ± 6d	0

Values within a row sharing different letters indicate significant differences in arrived or retained seeds between different life forms each time ($P < 0.05$).

Table 4
Arrived and retained seeds (grains m^{-2}) of different ecological groups. R: retained seeds, D: arrived seeds. Seed number is expressed as mean ± SE.

Bare patch	May–August								
	Psammophyte			Steppe species			Meadow species		
	R	D	Ratio	R	D	Ratio	R	D	Ratio
1	20 ± 6a	159 ± 19c	13%	0b	38 ± 30d	0	14 ± 6a	48 ± 7d	29%
2	17 ± 6a	444 ± 53c	4%	14 ± 5a	135 ± 29d	10%	14 ± 5a	108 ± 28d	13%
3	31 ± 10a	235 ± 32c	13%	7 ± 4a	343 ± 58c	1%	13 ± 7a	67 ± 33d	19%
4	21 ± 6a	368 ± 37c	6%	18 ± 5a	75 ± 19d	6%	54 ± 14b	138 ± 20e	39%
5	48 ± 12a	406 ± 31c	12%	0b	29 ± 11d	0	6 ± 4b	44 ± 11d	14%
6	23 ± 8a	702 ± 72c	3%	0b	40 ± 12d	0	30 ± 13a	83 ± 18e	36%
7	10 ± 5a	71 ± 13c	14%	0b	7 ± 4d	0	7 ± 4a	137 ± 58c	5%
8	20 ± 7a	202 ± 28c	10%	0b	11 ± 5d	0	38 ± 18a	207 ± 49c	18%
9	29 ± 8a	338 ± 34c	9%	0b	24 ± 11d	0	17 ± 7a	88 ± 27e	19%
10	31 ± 9a	226 ± 36c	14%	0b	0d		8 ± 4a	41 ± 21e	20%
11	56 ± 11a	475 ± 79c	12%	3 ± 3b	17 ± 6d	18%	31 ± 13a	72 ± 23e	43%

Bare patch	September–November								
	Psammophyte			Steppe species			Meadow species		
	R	D	Ratio	R	D	Ratio	R	D	Ratio
1	23 ± 7a	167 ± 44d	14%	1 ± 1b	8 ± 3e	13%	32 ± 10a	297 ± 56d	11%
2	9 ± 6a	292 ± 51d	3%	0a	15 ± 6e	0	17 ± 7a	330 ± 69d	5%
3	19 ± 10a	70 ± 37d	27%	0a	41 ± 32e	0	7 ± 4a	85 ± 30d	8%
4	54 ± 18a	246 ± 40d	22%	0b	13 ± 4e	0	21 ± 8c	166 ± 38d	13%
5	10 ± 7a	38 ± 11d	26%	2 ± 2a	0e		33 ± 18b	92 ± 19f	36%
6	21 ± 11a	62 ± 18d	34%	0b	0e		62 ± 19c	172 ± 58f	36%
7	17 ± 8a	68 ± 18d	25%	0a	7 ± 4e	0	5 ± 5a	263 ± 51f	2%
8	11 ± 7a	151 ± 29d	15%	0a	0e		44 ± 15c	420 ± 89f	10%
9	21 ± 15a	40 ± 13d	53%	0b	7 ± 4e	0	5 ± 3b	88 ± 23f	6%
10	5 ± 5a	41 ± 11d	12%	0a	3 ± 3e	0	10 ± 6a	105 ± 27f	10%
11	19 ± 12a	83 ± 28d	23%	0a	8 ± 5e	0	11 ± 9a	364 ± 75f	3%

Values within a row sharing different letters indicate significant differences in arrived or retained seeds between different ecological groups each time ($P < 0.05$).

Table 5
Correlation between CCA ordination axes and factors.

Factor	Axis	
	1	2
Area	0.0374	0.3447
Cover	−0.6942**	0.0412

** $P < 0.01$.

The retained seed:arrived seed ratio was generally less than 20%, regardless of patch size, investigation time, species life form and ecological group (Tables 2–4). The ratio was not closely related to patch size and investigation time (Table 2), but closely related to life form and ecological group (Tables 3 and 4).

From May to August, the arrived and retained seeds of annuals were 208–702 (grains m^{-2}) and 17–89 (grains m^{-2}), respectively; but for perennials, they were 0–350 (grains m^{-2}) and 0–14 (grains m^{-2}). From September to November, the arrived and retained seeds of annuals were 131–629 (grains m^{-2}) and 15–81 (grains m^{-2}), respectively; but for perennials, they were 0–43 (grains m^{-2}) and 0–2 (grains m^{-2}). The arrived and retained seeds of annuals were higher than those of perennials each time ($P < 0.05$) (Table 3). The ratio of annuals was generally higher than that of perennials in most cases at each investigation time too (Table 3).

In general, from May to August the arrived seeds was ranged in ascending order as psammophyte, meadow species and steppe species; the retained seeds of psammophyte or meadow species were higher than those of steppe species ($P < 0.05$) (Table 4). From May to August, the arrived seeds of meadow species were higher than those of psammophyte, whose were higher than those of steppe species; but the retained seeds of psammophyte, meadow species and steppe species were similar ($P > 0.05$) (Table 4). The ratio of psammophyte or meadow species was higher than that of steppe species in most cases at each investigation time (Table 4).

3.2. Relationship between the removed seeds and patch attributes

The first and second axes explained 7% and 5.1% of variation, respectively. The first one was strongly correlated with vegetation coverage. No significant correlation between patch area and the removed seeds was found (Table 5). Frequency of seeds with appendages decreased and those without appendages increased with the increase in vegetation coverage.

3.3. Relationship between the removed seeds and seed attributes

The first and second axes explained 45.2% and 12.7% of the variation, respectively. The first axis was strongly correlated with appendage and shape, and the second one weakly correlated with mass and shape (Table 6). Appendages adaptive to anemochory reduced seed retention probability. With the decrease in shape variance, more seeds stayed. No significant correlation between mass and seed loss was found.

Table 6
Correlation between CCA ordination axes and factors.

Factor	Axis	
	1	2
Weight	−0.0115	−0.1645
Appendage	0.9018***	0.0266
Shape	0.7468***	0.3822

*** $P < 0.001$.

4. Discussion

Low seed availability as well as the unfavorable microsite accounts for species' absence from bare patches (Bossuyt et al., 2004; Boulant et al., 2008; Brokaw and Busing, 2000). Low seed arrival, low seed capture or both lead to low seed availability. Our results showed that regardless of patch size, investigation time, species life form and ecological group, less than 20% of the arrived seeds were retained in the bare patch. Furthermore, the retained seeds in total were 39–168 (grains m^{-2}) for all patches from May to November (Table 2). Since only seeds arrived and retained from May to August (the germination season) contribute to vegetation restoration, and the retained seeds for all patches were 17–93 (grains m^{-2}) during this period, low seed availability is caused by low seed retention in the bare patches. Therefore, the hypothesis that low seed capture rather than low seed arrival accounts for low seed availability of bare patches is supported.

Arrival of seeds at inopportune time further explained low seed availability of the bare patches. Since the arrived or retained seeds during September to November were nearly equal to those during May to August (Table 2), more seeds would arrive or be retained during the non-germination season rather than the germination season if the period from December to next April was taken into consideration. It has been found that some species delay their seed release and a number of seeds disperse in the next year (Liu et al., 2006). Since seeds that arrive in the non-germination season contribute little to seed availability in the growing season due to predation and wind erosion, it seems that a large proportion of seeds arrive at inopportune time.

Although previous studies conducted in grasslands indicate that vegetation cover is closely linked to seed retention (Aguiar and Sala, 1997; Chambers et al., 1991), we found that vegetation cover was not so important (Table 5). In our opinion, two reasons lead to this difference. Firstly, previous studies determined the effect of vegetation cover on seed retention by comparing bare patches (vegetation cover is very low) and vegetation patches (vegetation cover is very high) between which there is a significant difference in vegetation cover, but we studied this issue by comparing bare patches with a limited range of vegetation cover (i.e., there is a small difference in vegetation cover among different bare patches). Secondly, difference in the vegetation cover among bare patches with a vegetation cover less than 10% is not significant enough to distinguish its effect on seed retention. Therefore, the fact that vegetation cover of bare patches explains seed retention weakly in our research does not indicate that vegetation cover is not important for seed retention (Aguiar and Sala, 1997). It does mean that when the vegetation coverage falls below a threshold, bare patches are able to capture few seeds and no significant difference in seed capture can be found among them.

Concerning effects of seed morphological traits on seed retention, we found that, contrary to previous conclusions (Fernandez et al., 2002; Chambers et al., 1991), seed mass is less important, but shape and appendage more important. Seed shape is correlated with surface area, which in turn determines wing loading, the ratio between seed weight and seed area (Matlack, 1987). For a given mass, flat and long seeds have low wing loading than spherical ones since the former probably has a large area than the latter. So, flat seeds are prone to disperse. The effect of seed shape on seed retention in our study can also be explained by the annuals/perennials ratio: more annual seeds were retained than perennial seeds in the bare patches (Table 3), and the former are closer to sphericity (Yan et al., 2005). Since adaptive appendages, i.e., hairs, wings and awns, promote seed dispersal but hamper seed retention (Van der Pijl, 1982), more seeds without appendages stay than those with them. Seeds of psammophytes do not have appendages (Yan et al., 2005), and they tended to be retained in the bare patch (Table 4).

Our results did not show that the smaller the seeds were, the more the seeds were retained (Chambers et al., 1991; Peart, 1979). Seed mass is evidently correlated with seed size (Azcarate et al., 2010), and seeds are captured when they are smaller than the soil particle. Most seeds captured by our traps were much larger than the soil particle, 75% of which falls in the class <1 mm (Zhang et al., 2009), so they were not able to be captured by the soil particle, and moved again after landing on patches. The large seeds were captured randomly, and there was no significant correlation between seed mass and seed retention when a threshold in soil particle is reached.

In comparison to the undegraded grassland (Aguiar and Sala, 1997; Jakobsson et al., 2006), the retained seed:arrived seed ratio was lower in the bare patch of the degraded grasslands. The partial reason may be that the capture ability becomes weak when soil particle has turned to sand and become smaller than arrived seeds.

Factors influencing seed arrival and retention affected the retained seed:arrived seed ratio. According to the above discussion, the ratio under the investigated patch scale was regulated by vegetation cover, seed shape and seed appendage, but was not regulated by patch size. Our study indicated that seed arrival was scale-independent, contrary to our prediction. The reasons remain unknown. Since previous studies show that the patch size has an effect on seed dispersal or seed retention (Munzbergova, 2004), more studies concerning effects of patch scale on seed dispersal and retention should be conducted.

This study examined only how seed availability is influenced by seed dispersal and retention. Determinants of vegetation restoration such as habitat limitation have not been considered. Further attention should be paid to factors relevant to seedling emergence and plant establishment in the bare patch of desertified grassland.

To conclude, (1) low seed capture mainly accounted for low seed availability in bare patches; (2) arrival of seeds at inopportune time further explained low seed availability in the patches; (3) vegetation cover, seed shape and seed appendage were the major factors regulating seed capture; (4) management for restoration should strengthen seed availability by raising seed retention.

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Appendix A.

A list of the entire species involved in the study. AH, annual herb; PH, perennial herb; S, shrub; P, psammophyte; M, meadow species; ST, steppe species. "–" means species not investigated (Liu et al., 2003, 2004; TCSIMNAR, 1985).

Species	Family	Life form	Ecological group	Mean mass per 100 seeds (mg)	Mean variance	Seed appendage
Puccinellia tenuiflora	Gramineae	PH	ST	7	0.124	No
Phragmites communis		PH	P,ST	31	0.167	No
Pappophorum boreale		AH	ST	55	0.109	Awn
Setaria viridis		AH	M	55	0.089	No
Chloris virgata		AH	M	56	0.133	Awn
Digitaria ciliaris		AH	M	107	0.127	No
Tragus bertesonianus		AH	M	–	–	Hook
Chenopodium acuminatum	Chenopodiaceae	AH	P	39	0.045	No
Agriophyllum squarrosum		AH	P	152	0.074	No
Corispermum candelabrum		AH	P	221	0.112	Wing
Inula britannica	Compositae	PH	ST	12	0.129	Pappus
Saussurea runcinata		PH	ST	158	0.135	Pappus
Caragana microphylla	Leguminosae	S	P	3324	0.047	No
Diarthron linifolium	Thymelaeaceae	AH	ST	–	–	No
Populus tomentos	Salicaceae	S	M	–	–	Hair
Saposhnikovia divaricata	Umbelliferae	PH	M	196	0.089	No
Tribulus terrestris	Zygophyllaceae	AH	M	13075	0.044	Spine
Ulmus pumila	Ulmaceae	S	ST	770	–	Wing

References

Aguiar, M.R., Sala, O.E., 1997. Seed distribution constrains the dynamics of the Patagonian steppe. Ecology 78, 93–100.

Arrieta, S., Suárez, F., 2005. Spatial dynamics of *Ilex aquifolium* populations seed dispersal and seed bank: understanding the first steps of regeneration. Plant Ecol. 177, 237–248.

Augspurger, C.K., Franson, S.E., 1987. Wind dispersal of artificial fruits varying in mass, area, and morphology. Ecology 68, 27–42.

Azcarate, F.M., Manzano, P., Peco, B., 2010. Testing seed-size predictions in Mediterranean annual grasslands. Seed Sci. Res. 20, 179–188.

Bossuyt, B., Honnay, O., Hermy, M., 2004. Scale-dependent frequency distributions of plant species in dune slacks: dispersal and niche limitation. J. Veg. Sci. 15, 323–330.

Boulant, N., Kunstler, G., Rambal, S., Lepart, J., 2008. Seed supply, drought, and grazing determine spatio-temporal patterns of recruitment for native and introduced invasive pines in grasslands. Divers. Distrib. 14, 862–874.

Brokaw, N., Busing, R.T., 2000. Niche versus chance and tree diversity in forest gaps. Trends Ecol. Evol. 15, 183–188.

Chambers, J.C., Macmahon, J.A., 1994. A day in the life of a seed-movements and fates of seeds and their implications for natural and managed systems. Annu. Rev. Ecol. Syst. 25, 263–292.

Chambers, J.C., Macmahon, J.A., Haefner, J.H., 1991. Seed entrapment in alpine ecosystems-effects of soil particle-size and diaspore morphology. Ecology 72, 1668–1677.

Chang, E.R., Veeneklaas, R.M., Buitenwerf, R., Bakker, J.P., Bouma, T.J., 2008. To move or not to move: determinants of seed retention in a tidal marsh. Funct. Ecol. 22, 720–727.

Debain, S., Curt, T., Lepart, J., 2003. Seed mass, seed dispersal capacity, and seedling performance in a *Pinus sylvestris* population. Ecoscience 10, 168–175.

Dreber, N., Esler, K.J., 2011. Spatio-temporal variation in soil seed banks under contrasting grazing regimes following low and high seasonal rainfall in arid Namibia. J. Arid Environ. 75, 174–184.

Emmerson, L., Facelli, J.M., Chesson, P., Possingham, H., 2010. Secondary seed dispersal of *Erodiophyllum elderi*, a patchily distributed short-lived perennial in the arid lands of Australia. Austral. Ecol. 35, 906–918.

Fernandez, R.J., Golluscio, R.A., Bisigato, A.J., Soriano, A., 2002. Gap colonization in the Patagonian semidesert: seed bank and diaspore morphology. Ecography 25, 336–344.

Greene, D.F., Johnson, E.A., 1993. Seed mass and dispersal capacity in wind-dispersed diaspores. Oikos 67, 69–74.

Günster, A., 1994. Seed bank dynamics—longevity, viability and predation of seeds of serotinous plants in the central Namib Desert. J. Arid Environ. 28, 195–205.

Jakobsson, A., Eriksson, O., Bruun, H.H., 2006. Local seed rain and seed bank in a species-rich grassland: effects of plant abundance and seed size. Can. J. Bot. 84, 1870–1881.

Kalamees, R., Zobel, M., 2002. The role of the seed bank in gap regeneration in a calcareous grassland community. Ecology 83, 1017–1025.

Kassas, M., 1995. Desertification—a general-review. J. Arid Environ. 30, 115–128.

King, T.J., 2007. The roles of seed mass and persistent seed banks in gap colonisation in grassland. Plant Ecol. 193, 233–239.

Klausmeier, C.A., 1999. Regular and irregular patterns in semiarid vegetation. Science 284, 1826–1828.

Kotanen, P.M., 1997. Effects of gap area and shape on recolonization by grassland plants with differing reproductive strategies. Can. J. Bot. 75, 352–361.

Liu, Z.M., 2010. Plant Regenerative Strategies in the Horqin Sand Land. China Meteorological Press, Beijing, pp. 4–14 (in Chinese).

Li, S.G., Yoshinobu, H., Takehisa, O., Zhao, H.L., He, Z.Y., Chang, X.L., 2000. Grasslanddesertification by grazing and the resultingmicrometeorologicalchanges in InnerMongolia. Agr. Forest Meteoro. 102 (2–3), 125–137.

Liu, Z.M., Li, X.H., Li, R.P., Luo, Y.M., Wang, H.M., Jiang, D.M., Nan, Y.G., 2003. A comparative study on diaspore shape of 70 species in the sandy land of Horqin. Acta Pratacult. Sin. 12 (5), 55–61 (in Chinese with English abstract).

Liu, Z.M., Li, R.P., Li, X.H., Luo, Y.M., Wang, H.M., Jiang, D.M., Nan, Y.G., 2004. A comparative study of seed weigh of 69 plant species in Horqin Sandyland. Chin. J. Plant Ecol. 28, 225–230 (in Chinese with English abstract).

Liu, Z.M., Yan, Q.L., Baskin, C.C., Ma, J.L., 2006. Burial of canopy-stored seeds in the annual psammophyte *Agriophyllum squarrosum* Moq. (Chenopodiaceae) and its ecological significance. Plant Soil 288, 71–80.

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

Ma, J.L., Liu, Z.M., 2008. Spatiotemporal pattern of seed bank in the annual psammophyte *Agriophyllum squarrosum* Moq. (Chenopodiaceae) on the active sand dunes of northeastern Inner Mongolia, China. Plant Soil 311, 97–107.

Matlack, G.R., 1987. Diaspore size, shape, and fall behavior in wind-dispersed plant species. Am. J. Bot. 74, 1150–1160.

Miller, T.E., 1982. Community diversity and interactions between the size and frequency of disturbance. Am. Nat. 120, 533–536.

Munzbergova, Z., 2004. Effect of spatial scale on factors limiting species distributions in dry grassland fragments. J. Ecol. 92, 854–867.

Panetta, F.D., Wardle, D.A., 1992. Gap size and regeneration in a New Zealand dairy pasture. Aust. J. Ecol. 17, 169–175.

Peart, M.H., 1979. Experiments on the biological significance of the morphology of seed-dispersal units in grasses. J. Ecol. 67, 843–863.

Team for Comprehensive Surveying in Inner Mongolia and Ningxia Autonomous Regions (TCSIMNAR), 1985. Vegetation in Inner Mongolia. Science Press, Beijing (in Chinese).

Van der Pijl, 1982. Principles of Dispersal in Higher Plants. Springer, Berlin, Heidelberg, New York.

Wang, X.M., Chen, F., Hasi, E., Li, J.C., 2008. Desertification in China: an assessment. Earth-Sci. Rev. 88, 188–206.

Yan, Q.L., Liu, Z.M., Li, R.P., Luo, Y.M., Wang, H.M., 2005. Relationship between seed production, seed morphology and plant life form in 75 species in Horqin Steppe. Acta Pratacult. Sin. 14 (4), 21–28 (in Chinese with English abstract).

Yan, Q.L., Liu, Z.M., Ma, J.L., Jiang, D.M., 2007. The role of reproductive phenology, seedling emergence and establishment of perennial Salix gordejevii in active sand dune fields. Ann. Bot. 99, 19–28.

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. Environ. Earth Sci. 58, 615–624.

Zhang, J.Y., Wang, J., Zhao, H.L., 2009. Changes in soil particles fraction and its spatial variation characteristics in restoration processes of sandy desertification land. J. Soil Water Conserv. 23 (3), 153–157 (in Chinese with English abstract).

Zhao, H.L., Zhang, T.H., Zhao, X.Y., Toshiya, O., Zhou, R.L., 2002. Sand desertification processes of over-grazing pasture in Inner Mongolia. Arid Zone Res. 19 (4), 1–6 (in Chinese with English abstract).