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Spatiotemporal characteristics of seed rain and soil seed bank of artificial *Caragana korshinskii* Kom. forest in the Tengger Desert, China

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Abstract: Vegetation restoration and reconstruction are effective approaches to desertification control and achieving social and economic sustainability in desert areas. However, the self-succession ability of native plants during the later periods of vegetation restoration remains unclear. Therefore, this study was conducted to bridge the knowledge gap by investigating the regeneration dynamics of artificial forest under natural conditions. The information of seed rain and soil seed bank was collected and quantified from an artificial *Caragana korshinskii* Kom. forest in the Tengger Desert, China. The germination tests were conducted in a laboratory setting. The analysis of species quantity and diversity in seed rain and soil seed bank was conducted to assess the impact of different durations of sand fixation (60, 40, and 20 a) on the progress of vegetation restoration and ecological conditions in artificial *C. korshinskii* forest. The results showed that the top three dominant plant species in seed rain were *Echinops gmelinii* Turcz., *Eragrostis minor* Host., and *Agropyron mongolicum* Keng., and the top three dominant plant species in soil seed bank were *E. minor*, *Chloris virgata* Sw., and *E. gmelinii.* As restoration period increased, the density of seed rain and soil seed bank increased first and then decreased. While for species richness, as restoration period increased, it gradually increased in seed rain but decreased in soil seed bank. There was a positive correlation between seed rain density and soil seed bank density among all the three restoration periods. The species similarity between seed rain or soil seed bank and aboveground vegetation decreased with the extension of restoration period. The shape of the seeds, specifically those with external appendages such as spines and crown hair, clearly had an effect on their dispersal, then resulting in lower seed density in soil seed bank. In addition, precipitation was a crucial factor in promoting rapid germination, also resulting in lower seed density in soil seed bank. Our findings provide valuable insights for guiding future interventions during the later periods of artificial *C. korshinskii* forest, such as sowing and restoration efforts using unmanned aerial vehicles.

Keywords: ecological restoration; soil seed bank; seed rain; artificial forest; vegetation desertification; *Caragana korshinskii*; Tengger Desert

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1 Introduction

Artificial sand fixation vegetation construction can improve the structure and physicochemical properties of soil in desert areas, effectively controlling desertification process (Liu et al., 2011; Li et al., 2014). *Caragana korshinskii* Kom., a large deciduous shrub in Leguminosae that has developed roots and deep taproots and is resistant to drought and temperature extremes, is an excellent sand-fixing plant species for desert areas (Xie et al., 2014). Changes in seed rain and soil seed bank of artificial *C. korshinskii* forests reflect the degree of ecological restoration: the more complex the composition, the better the stability of ecosystem (Houerou, 2000; Zhao et al., 2019). Therefore, it is important to study these changes in seed rain and soil seed bank to optimize artificial sand fixation vegetation construction and ecological restoration.

In recent years, numerous studies have been conducted on the spatiotemporal variation of seed rain and soil seed bank in arid areas. Dreber and Esler (2011) demonstrated that despite environmental degradation, secondary dispersal and seed retention are still effectively regulated. Moreover, the timing and sequence of rainfall seasons in previous years may exert a profound influence on soil seed banks. Liu et al. (2021) revealed that soil seed banks facilitate vegetation restoration in *Salix* communities located on the southeastern edge of Mu Us Sandy Land in China. In addition, vegetation growth after restoration is known to significantly increase soil clay and silt content (Luo et al., 2019), increase soil water content (Li et al., 2007), accumulate soil carbon and nitrogen continuously (Li et al., 2018), increase soil microbial biomass and enzyme activity, improve soil texture effectively, and promote the formation of soil biological crust (Li et al., 2016), resulting in improved topsoil water retention, enhanced soil stability, and an altered surface micromorphology (Sonkoly et al., 2017). However, as restoration progresses, the thickening of soil biological crust prevents the deep penetration of precipitation into soil (Kakeh et al., 2020). Along with an increase in vegetation restoration period, the deep soil water content decreases, whereas the competition for water by drought-tolerant plants with deep roots intensifies. Consequently, some deep-rooted plants would decrease in number or even withdraw from community (Zhao et al., 2022).

Seeds play a crucial role in the natural regeneration of plants (Nathan and Muller-Landau, 2000) and have a stronger tolerance to harsh environments than adult plants. Seeds have an impact on individual reproduction, population expansion, the recovery of damaged populations, species resistance to adverse environments, and gene pool preservation (Wang and Malanson, 2008; Dreber and Esler, 2011). Seed rain refers to the process by which seeds disperse from mother plants to ground through gravity or external forces (Kim et al., 2022), serving as the primary source for forest community renewal and reproduction (de Heredia et al., 2015). A soil seed bank comprises all viable seeds that present in soil surfaces or substrates (Amiaud and Touzard, 2004). When vegetation is disturbed or damaged by external factors, buried seeds can assist in vegetation recovery and population continuation; thus, they act as a buffer against species extinction (Long et al., 2015). This survival strategy has evolved over time and is crucial in desert areas where living conditions are extremely challenging (Wang et al., 2020). Biological and abiotic factors determine the spatiotemporal dynamics of seed rain and soil seed bank (Webb et al., 2006; Lowe and Mcpeek, 2014). Specifically, temporal dynamics are influenced by biological factors such as species phenological period and tree age, as well as abiotic factors such as temperature and soil water content; in contrast, spatial dynamics are generally considered to be highly stochastic (Lu et al., 2019), owing to various processes that affect seed dispersal including community species composition, the distribution of mother plants, seed dispersal mode, and the interactions with animals for feeding or transport (Martini and dos Santos, 2007). Research on seed rain and soil seed bank revealed the relationship between the period of sand fixation and plant sexual reproduction and helped to predict the trend of vegetation regeneration and succession (Wang, 2002). It is also useful in determining the optimal flight sowing dates (using unmanned aerial vehicles) and quantities for fly-sowing afforestation. These findings have had significant implications for researching plant community renewal dynamics and have facilitated vegetation restoration efforts (de Andrés et al., 2014).

Existing studies have mainly discussed the effects of soil physical and chemical properties on the diversity characteristics of soil seed bank. Studies on changes in the relationship between seed rain and soil seed bank and the period of restoration, however, have been somewhat lacking. In particular, information on the self-succession ability of native plants during the later stages of vegetation restoration is scarce. Therefore, the current study assessed the self-succession potential of the artificial *C. korshinskii* forest within the Tengger Desert with different periods of vegetation restoration. The following items were considered in this study: (1) variations in the numbers and composition of seed rain among different restoration periods; (2) characteristics of soil seed bank diversity across different periods after restoration; (3) relationships among seed rain, soil seed bank, and aboveground vegetation; (4) spatiotemporal dynamics of seed rain and soil seed bank of artificial *C. korshinskii* forest. These investigations enabled us to understand the changes occurred in the species composition of seed rain and soil seed bank over time during vegetation recovery process in *C. korshinskii* forest. The novelty of this study is the selection of sampling plots at different restoration periods. In addition, long time series of plots were formed to study the effects of different restoration periods on seed rain and soil seed bank.

2 Materials and methods

2.1 Study area

The Tengger Desert, which is mainly situated in the southeastern part of Alagxa Left Banner, Alagxa League, Inner Mongolia Autonomous Region, China, is one of the four major deserts in China, with an elevation of approximately 1200–1400 m. The study area (37°25′58″–37°37′24″N, 104°49′25″–105°09′24″E) is located within the Shapotou artificial sand-fixing area in Zhongwei City, Ningxia Hui Autonomous Region, China. It lies on the southeastern edge of the Tengger Desert and comprises a steppe desert zone and a transition zone between desert and oasis. The local climate is temperate continental with the characteristics of steppe desert, including limited rainfall, high evaporation rates, and significant temperature fluctuations between cold and hot seasons that are ascribed to the influence of high-pressure systems originating in Mongolia Plateau. The average annual temperature is 9.6°C, and the average annual precipitation is approximately 186.600 mm with considerable variation in precipitation levels throughout the year. Prevailing winds are from the southwest to northwest, and strong gusts are common throughout the year. The average annual wind speed is approximately 4.1 m/s. The prevalent soil type is aeolian sand characterized by low soil water content (approximately 0.60%), relatively high soil bulk density (about 1.60 g/cm^3), and a slightly alkaline pH value (about 7.5). Fine sand particles (0.050–0.250 mm) comprise more than 84.0% of the mechanical composition of soil in the study area, whereas physical viscous particles (0.002–0.050 mm) and coarse sand particles (>0.250 mm) are scarce, leading to good permeability but loose soil structure and making the land susceptible to erosion. The soil around the Baotou-Lanzhou Railway in Inner Mongolia Autonomous Region is a good example. Since 1957, artificial sand consolidation protection belts have been established on both sides of the railway line to safeguard it against wind erosion and sand burial (Fullen and Mitchell, 1994). The dominant species of study area is *C. korshinskii*, with *Echinops gmelinii* Turcz. and *Setaria viridis* (L.) P. Beauv. being the main herbaceous plants. The total vegetation coverage is approximately 3.00%. The other plant species covered in the study area are *Eragrostis minor* Host, *Chloris virgata* Sw., *Salsola collina* Pall., *Bassia dasyphylla* (Fisch. et Mey.) O. Kuntze, *Artemisia scoparia* Waldst. et Kit., *Artemisia arenaria* DC., *Agriophyllum squarrosum* (L.) Moq., *Corispermum mongolicum* Iljin, and *Agropyron mongolicum* Keng.

2.2 Methods

2.2.1 Sampling design and measurements of soil physical and chemical properties

Three artificial *C. korshinskii* stands established in 1964 (restoration period almost reached 60 a), 1982 (restoration period was 40 a), and 2002 (restoration period was 20 a) were selected from the study area. The stands have similar altitude, slope, and habitat characteristics. Each stand consisted of four sampling plots measuring 20 m×20 m, resulting in twelve sampling plots in total. Three random sampling points were selected within each sampling plot to collect soil samples from three different soil layers at depths of 0.0–10.0, 10.0–20.0, and 20.0–30.0 cm. After mixing soil and deionized water with the ratio of 1:5, we measured soil pH and electrical conductivity (EC) by SG78-ELK-ISM (Mettler-Toledo Instruments (Shanghai) Co., Ltd. Shanghai, China). After leaching the soil samples with NH_4OAc, we measured available potassium (AK) by BWB XP Flame Photometer (BWB Technologies Ltd., Newbury, Berkshire, the UK). Based on Bao (2000), we determined soil total nitrogen (TN) by automatic semi-micro Kjeldahl method, measured available phosphorus (AP) by molybdenum-antimony anti-spectrophotometric method, and detected total organic matter (TOM) by potassium dichromate method. Table 1 summarizes the soil physical and chemical properties measured in each stand at each layer, and Table 2 provides an overview of the stand characteristics observed within sample plots.

Table 1 Physical and chemical properties of soil samples collected from artificial *Caragana korshinskii* forest at different restoration periods

Property	Soil layer (cm)	Restoration period		
		60 a	40 a	20 a
Electrical conductivity (EC; μS/cm)	0.0–10.0	211.28±82.71^{Aa}	51.67±3.56^{Ba}	40.29±7.21^{Ba}
	10.0–20.0	84.30±16.98^{Aa}	51.62±3.89^{Aa}	47.58±15.65^{Aa}
	20.0–30.0	69.89±10.75^{Aa}	46.36±5.31^{Aa}	42.90±16.22^{Aa}
Total organic matter (TOM; g/kg)	0.0–10.0	8.29±0.31^{Aa}	4.51±0.63^{Ba}	6.64±0.45^{Ca}
	10.0–20.0	6.40±0.39^{Ab}	4.03±0.16^{Ba}	5.22±0.63^{ABab}
	20.0–30.0	4.73±0.55^{Ac}	3.33±0.40^{Ba}	4.63±0.25^{ABb}
Total nitrogen (TN; g/kg)	0.0–10.0	0.19±0.02^{Aa}	0.09±0.02^{Ba}	0.09±0.02^{Ba}
	10.0–20.0	0.16±0.01^{Aa}	0.08±0.01^{Ba}	0.09±0.01^{Ba}
	20.0–30.0	0.10±0.01^{Ab}	0.05±0.02^{Ba}	0.08±0.01^{ABa}
Available potassium (AK; mg/kg)	0.0–10.0	109.03±6.49^{Aa}	105.08±2.28^{ABa}	89.45±6.24^{Ba}
	10.0–20.0	97.82±4.77^{Aab}	98.85±8.86^{Aab}	80.45±4.31^{Aa}
	20.0–30.0	82.40±5.08^{Ab}	85.99±3.15^{Ab}	82.33±7.49^{Aa}
Available phosphorus (AP; mg/kg)	0.0–10.0	34.78±3.87^{Aa}	23.25±2.26^{Ba}	18.93±2.45^{Bb}
	10.0–20.0	22.29±2.35^{Ab}	10.44±1.26^{Bb}	22.77±1.06^{Aa}
	20.0–30.0	16.523±3.40^{Ab}	14.92±1.47^{Ab}	11.72±1.74^{Ab}
pH	0.0–10.0	8.97±0.02^{Ab}	8.72±0.15^{Aa}	8.80±0.15^{Aa}
	10.0–20.0	9.08±0.03^{Aa}	8.68±0.17^{Aa}	8.78±0.13^{Aa}
	20.0–30.0	9.02±0.02^{Aab}	8.53±0.20^{Aa}	8.67±0.22^{Aa}

Note: Different uppercase letters in the same row indicate that there is a significant difference at $P<0.05$ level among different stands, and different lowercase letters in the same column indicate that there is a significant difference at $P<0.05$ level among different soil layers.

2.2.2 Seed rain survey

A seed rain collector was used in this study, consisting of a plastic funnel with an inner diameter of 20.0 cm, a bottomless plastic cylinder with a diameter of 20.0 cm, and a gauze bag (Fig. 1). The collector was designed and built independently. The 20.0 cm diameter funnel facilitated the rapid falling of collected seeds into gauze bag and prevented these seeds from flying out. There was a gap of approximately 5.0 cm between the bottom of gauze bag and the lower soil. Therefore, rain falling in the collector can directly penetrate into soil through gauze, thus preventing the collected seeds from rotting due to excessive moisture. The plastic cylinder was fixed vertically to the ground, and the edge of funnel was 1.0 cm above the soil surface to prevent runoff from soil or rainfall around the funnel from entering the collector.

A typical grid method was used to arrange 25 seed rain collectors evenly in each sampling plot at intervals of 5.0 m, with a total of 300 seed rain collectors used in the 12 sampling plots.

Table 2 Species composition of artificial *C. korshinskii* forest at different restoration periods

Restoration period	Sampling plot	Number of *C. korshinskii* plants	Species composition
60 a	Y1–1	38	*C. korshinskii*, *E. gmelini*, *E. minor*, *C. virgata*, *S. viridis*, *S. collina*, *B. dasyphylla*, *A. arenaria*, and *A. scoparia*
	Y1–2	42	*C. korshinskii*, *E. gmelinii*, *E. minor*, *S. viridis*, *C. virgata*, *S. collina*, *A. scoparia*, *A. arenaria*, *A. squarrosum*, and *B. dasyphylla*
	Y1–3	46	*C. korshinskii*, *E. gmelinii*, *E. Minor*, *C. Virgata*, *S. Collina*, *S. Viridis*, *A. mongolicum*, and *B. dasyphylla*
	Y1–4	35	*C. korshinskii*, *E. gmelinii*, *E. minor*, *S. viridis*, *C. virgata*, *S. collina*, *A. scoparia*, *A. mongolicum*, and *B. dasyphylla*
40 a	Y2–1	41	*C. korshinskii*, *E. gmelinii*, *E. minor*, *S. viridis*, *C. virgata*, *S. collina*, *A. scoparia*, and *B. dasyphylla*
	Y2–2	42	*C. korshinskii*, *E. gmelinii*, *E. minor*, *S. viridis*, *C. virgata*, *S. collina*, *A. scoparia*, and *B. dasyphylla*
	Y2–3	39	*C. korshinskii*, *E. gmelinii*, *C. virgata*, *E. minor*, *S. viridis*, *S. collina*, *A. arenaria*, *A. scoparia*, and *B. dasyphylla*
	Y2–4	37	*C. korshinskii*, *E. gmelinii*, *C. virgata*, *E. minor*, *S. viridis*, *S. collina*, *A. arenaria*, *A. scoparia*, and *B. dasyphylla*
20 a	Y3–1	41	*C. korshinskii*, *E. gmelinii*, *C. virgata, E. Minor*, *S. Viridis*, *B. Dasyphylla*, and *Corispermum mongolicum*
	Y3–2	38	*C. korshinskii*, *E. gmelinii*, *E. minor*, *C. virgata*, *B. Dasyphylla*, *Corispermum mongolicum*, *S. viridis*, *A. arenaria*, and *S. collina*
	Y3–3	45	*C. korshinskii*, *E. gmelinii*, *B. Dasyphylla*, *E. minor*, *S. viridis*, and *S. collina*
	Y3–4	39	*C. korshinskii*, *E. gmelinii*, *E. minor*, *B. Dasyphylla*, *Corispermum Mongolicum*, *S. collina*, and *A. scoparia*

Note: *C. korshinskii*, *Caragana korshinskii* Kom.; *E. gmelinii*, *Echinops gmelinii* Turcz.; *E. minor*, *Eragrostis minor* Host; *C. virgata*, *Chloris virgata* Sw.; *S. viridis*, *Setaria viridis* (L.) P. Beauv.; *S. collina*, *Salsola collina* Pall.; *B. dasyphylla*, *Bassia dasyphylla* (Fisch. et Mey.) O. Kuntze; *A. mongolicum*, *Agropyron mongolicum* Keng; *A. arenaria*, *Artemisia arenaria* DC.; *A. scoparia*, *Artemisia scoparia* Waldst. et Kit.; *A. squarrosum*, *Agriophyllum squarrosum* (L.) Moq.; *Corispermum mongolicum*, *Corispermum mongolicum* Iljin. Species are listed in descending order with respect to the number of species.

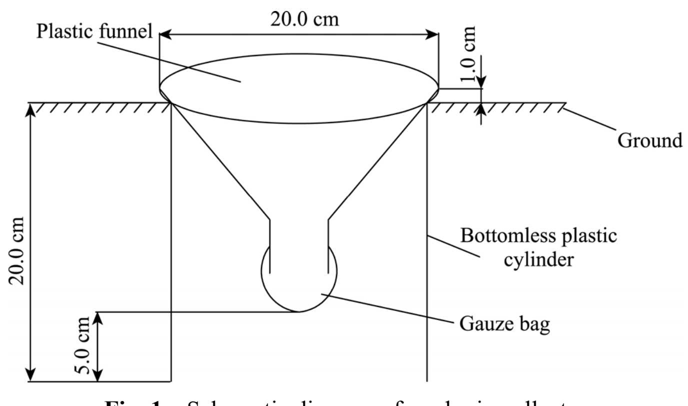

Fig. 1 Schematic diagram of seed rain collector

All the seed rain collectors were established by the end of April 2021. From 10 May 2021, the gauze bags were collected and replaced every 15 d. The bags were tied tightly, labeled with numbers, and transported to laboratory. Seed rain samples were sieved through a 2.000 mm mesh to separate large seeds from withered branches, leaves, and sandy soil. The screened seeds were identified and compared with reference specimens to determine the species composition of collected seeds. Considering the potential presence of small herbaceous seeds in residual soil samples, only seeds larger than 2.000 mm in diameter were air-dried, identified, and stored in ziplock bags with unique number. The remaining seed samples were assigned to germination experiment using soil samples collected as a medium.

Seed rain samples were distributed evenly in a germination box with a diameter of 12.0 cm and a height of 5.0 cm. The bottom of germination box was pre-filled with an approximately 2.5 cm thick layer of sterile fine sand as a substrate. Three additional germination boxes filled with sterile fine sand without seeds were used as control groups. The germination experiment was conducted in an artificial climate chamber set at a temperature of 25°C and a relative humidity of 60.00%. After sprout emergence, daily records were recorded for each sprouted seedling until no new seedlings appeared for two consecutive weeks, after which gibberellin was applied to break seed dormancy and promote further germination. The germination experiment was ended when no new seedlings emerged for two consecutive weeks after the application of gibberellin. The total number of species and the number of seedlings per germination box were tallied, and the number of harvested seedlings was converted to represent the density of seed rain within an area equivalent to 1.0 m^2.

2.2.3 Soil seed bank survey

The field experiment was conducted from 10 May 2021 to 10 November 2021. Five-point sampling method was used in the soil seed bank survey, and stratified sampling was conducted using cube steel soil seed bank samplers with dimensions of 20.0 cm×20.0 cm (0.0–2.0, 2.0–5.0, 5.0–10.0, and 10.0–20.0 cm) for bagging and subsequent laboratory analysis. The species composition of soil seed bank was determined using a direct germination experiment. After sifting the soil seed bank samples to a particle size of 2.000 mm and thoroughly mixing them, equal amounts of soil seed bank samples collected from each soil layer were spread evenly in germination boxes (29.0 cm×22.0 cm×7.5 cm) to an approximate thickness of 1.5 cm. A base layer comprising sterile fine sand, approximately 4.0 cm in thickness, was pre-loaded at the bottom of each germination box. Control measures were implemented using three additional germination boxes filled with sterile fine sand but without seeds. Germination experiment was conducted in the same manner as described in Section 2.2.2 above.

2.2.4 Aboveground vegetation survey

A diagonal random quadrat investigation of vegetation communities was conducted to prevent sample destruction, with each test sample setting to a quadrat size of 1.0 m×1.0 m. The following vegetation parameters were obtained: relative coverage, relative height, species richness, and biomass estimation; of which relative coverage was measured by photographic method (Zhang et al., 2003) and relative height was measured by direct measurement. All aboveground plants in the sampling quadrats were directly weighed by harvesting method and converted to biomass per unit area.

2.2.5 Data processing

The number of collected seeds and germinated seedlings was converted into seed density per square meter. The Sorensen formula was used to calculate the coefficient of similarity (McCreadie and Adler, 2018).

$$C_s = \frac{2j}{a+b}, \tag{1}$$

where C_s is the coefficient of similarity (%); j is the number of common species in community A and B; a is the total number of species contained in community A; and b is the total number of species contained in community B.

The importance value, which is used to represent the relative importance of plant species in a community, could be calculated as follows:

$$\text{IV} = \left(\frac{\text{RF+RC+RD}}{3}\right), \tag{2}$$

$$\text{RF} = \frac{f_i}{\sum_{i=1}^{n} f_i}, \tag{3}$$

$$\mathrm{RC}=\frac{c_i}{\sum_{i=1}^{n} c_i}, \tag{4}$$

$$\mathrm{RD}=\frac{a_i}{\sum_{i=1}^{n} a_i}, \tag{5}$$

where IV is the importance value of one species; RF is the relative frequency; RC is the relative coverage; RD is the relative density; f_i is the frequency of the i^{th} species; c_i is the sum of coverage area of the i^{th} species; a_i is the number of the i^{th} species; and n is the total number of species.

The statistical analysis of data was performed using SPSS 23.0 software (SPSS Inc., Chicago, Illinois State, the USA). The single factor analysis of variance (ANOVA) was employed to assess the differences in seed rain, soil seed bank, and aboveground vegetation across different restoration periods. Duncan's multiple test was used to determine the significance of these differences (α=0.05). Data visualization was conducted using Origin 2021 (Originlab Corporation, Northampton, Massachusetts State, the USA).

3 Results

3.1 Composition of seed rain

We evaluated the species richness of artificial *C. korshinskii* forest according to the composition of species in seed rain. The temporal trend of species richness can serve as an indicator for the stability and ecological restoration of artificial forest ecosystem. In this study, we analyzed the composition of seed rain in artificial *C. korshinskii* forest at different restoration periods (Table 3). The seed rain comprised 16 species from 7 families and 16 genera. The seeds of annual herbs made up the largest proportion, and their importance values were 85.44%, 90.01%, and 92.27% for *C. korshinskii* forest at restoration period of 60, 40, and 20 a, respectively. As restoration period increased, the proportion of annual herb seeds gradually decreased, whereas that of perennial plant seeds gradually increased. Among shrubs, *C. korshinskii* had the highest number of seeds in 40 a restoration period sampling plots. The seed rain in the sampling plots after recovering 60 a comprised 14 plant species from 7 families and 14 genera, with density reaching 2920.37 seeds/m^2. The top three important seeds identified were *E. gmelinii*, *E. minor*, and *A. mongolicum*. The seed rain in the 40 a restoration period sampling plots comprised 13 plant species belonging to 5 families and 13 genera. The seed rain density was 3580.59 seeds/m^2, with *E. gmelinii*, *A. mongolicum*, and *Corispermum mongolicum* having the most abundant seeds. In contrast, the seed rain in the 20 a restoration period sampling plots comprised only 10 plant species from 4 families and 10 genera. Its seed rain density was low (2467.09 seeds/m^2), with *E. gmelinii*, *S. collina*, and *C. virgata* being the top three contributors to the total amount of seeds. As restoration period increased, a gradual increase occurred in the number of species; however, the number of seeds in seed rain increased first and then decreased. The total seed rain density in the 40 a restoration period sampling plots was significantly greater than those in the 60 and 20 a sampling plots (P<0.05). The abundance of *E. gmelinii*, *C. korshinskii*, and *C. mongolicum* Iljin seeds in the 40 a restoration period sampling plots was significantly higher than those in the 60 and 20 a sampling plots (P<0.05). The abundance of *E. minor* and *A. mongolicum* seeds in the 60 a restoration period sampling plots was significantly higher than those in both the 40 and 20 a sampling plots (P<0.05). The abundance of *S. collina* and *C. virgata* seeds in the 20 a restoration period sampling plots was significantly higher than those in the 60 and 40 a sampling plots (P<0.05).

3.2 Temporal dynamic of seed rain

The temporal dynamic of seed rain in artificial *C. korshinskii* forest at different restoration periods exhibited a distinct 'double peak' pattern, as shown in Figure 2. Seed dispersal began to

Table 3 Composition of seed rain of artificial *C. korshinskii* forest at different restoration periods

Species	Family	Genus	Life form	60 a		40 a		20 a	
				Seed density (seeds/m^2)	Importance value (%)	Seed density (seeds/m^2)	Importance value (%)	Seed density (seed/m^2)	Importance value (%)
E. gmelinii	Compositae	*Echinops*	Annual herb	1647.13 ± 37.81^{b}	56.40	2693.63 ± 194.83^{a}	75.23	1496.82 ± 237.66^{b}	60.67
E. minor	Poaceae	*Eragrostis*	Annual herb	451.59 ± 102.68^{a}	15.46	150.64 ± 28.51^{b}	4.21	228.87 ± 33.23^{b}	9.28
A. mongolicum	Poaceae	*Agropyron*	Perennial herb	314.97 ± 128.54^{a}	10.79	233.76 ± 28.78^{ab}	6.53	162.21 ± 15.58^{b}	6.57
S. collina	Chenopodiaceae	*Salsala*	Annual herb	211.78 ± 112.79^{ab}	7.25	147.77 ± 23.11^{b}	4.13	303.18 ± 45.77^{a}	12.29
C. virgata	Poaceae	*Chloris*	Annual herb	167.83 ± 36.82^{ab}	5.75	64.65 ± 18.62^{b}	1.81	236.94 ± 64.68^{a}	9.60
C. korshinskii	Leguminosae	*Caragana*	Shrub	89.49 ± 63.55^{a}	3.06	114.97 ± 26.73^{a}	3.21	15.29 ± 8.59^{b}	0.62
A. desertorum	Chenopodiaceae	*Artemisia*	Perennial herb	15.92 ± 5.16^{a}	0.55	8.28 ± 2.11^{a}	0.23	12.31 ± 2.10^{a}	0.50
Corispermum mongolicum	Chenopodiaceae	*Corispermum*	Annual herb	10.51 ± 10.09^{b}	0.36	159.87 ± 80.20^{a}	4.46	2.55 ± 1.04^{b}	0.10
S. viridis	Poaceae	*Setaria*	Annual herb	5.41 ± 2.51^{a}	0.19	4.78 ± 2.77^{a}	0.13	8.07 ± 2.17^{a}	0.33
I. dentatum	Compositae	*Ixeridium*	Perennial herb	4.14 ± 3.73^{a}	0.14	-	-	0.85 ± 0.60^{a}	0.03
A. squarrosum	Chenopodiaceae	*Agriophyllum*	Annual herb	0.64±0.64	0.02	0.96±0.61	0.03	-	-
D. heterophyllum	Labiatae	*Dracocephalum*	Perennial herb	0.32±0.32	0.01	0.64±0.37	0.02	-	-
A. bidentatum	Liliaceae	*Allium*	Perennial herb	0.32±0.32	0.01	-	-	-	-
B. dasyphylla	Chenopodiaceae	*Bassia*	Annual herb	-	-	0.32±0.32	0.01	-	-
Calligonum mongolicum	Chenopodiaceae	*Calligonum*	Shrub	-	-	0.32±0.32	0.01	-	-
C. tenella	Cruciferae	*Chorispora*	Annual herb	0.32±0.32	0.01	-	-	-	-
Total				2920.37 ± 214.59^{ab}	100.00	3580.59 ± 265.83^{a}	100.00	2467.09 ± 350.64^{b}	100.00

Note: Different lowercase letters for the same species indicate significant differences among different restoration periods at $P<0.05$ level. "-" means no data. *A. desertorum*, *Artemisia desertorum* Spreng.; *I. dentatum*, *Ixeridium dentatum* (Thunb.) Tzvelev; *D. heterophyllum*, *Dracocephalum heterophyllum* Benth.; *A. bidentatum*, *Allium bidentatum* Fisch. ex Prokh.; *Calligonum mongolicum*, *Calligonum mongolicum* Turcz.; *C. tenella*, *Chorispora tenella* (Pall.) DC.

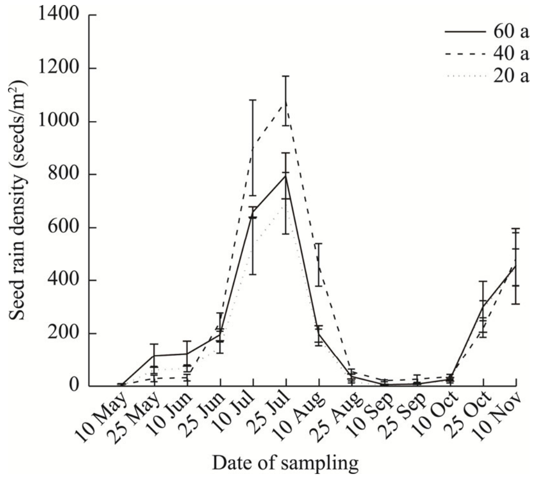

Fig. 2 Temporal dynamic of seed rain density of artificial *Caragana Korshinskii* Kom. forest at different restoration periods. Bars are standard errors.

spread in early May and gradually increased until the end of July. During this period, the seed rain densities were 794.90, 1077.07, and 691.72 seeds/m^2 for 60, 40, and 20 a restoration periods, respectively. Subsequently, seed rain density decreased to the lowest values in early September. After approximately 30 d, another increase of seed rain density was observed from early October to early November, with 453.82, 480.25, and 448.41 seeds/m^2 for 60, 40, and 20 a restoration periods, respectively.

3.3 Composition of soil seed bank

As shown in Table 4, 12 species belonging to 4 families and 12 genera were identified in the soil seed bank of artificial *C. korshinskii* forest. The proportions of annual herb seeds in artificial *C. korshinskii* forest at restoration periods of 60, 40, and 20 a were 98.09%, 99.12%, and 98.09%, respectively. The soil seed bank of artificial *C. korshinskii* forest at restoration period of 60 a comprised 9 plant species from 4 families and 9 genera with a total density of 4392.50 seeds/m^2, and the three most abundant seeds were *E. minor* (47.41%), *C. virgata* (34.49%), and *E. gmelinii* (7.74%). The soil seed bank of artificial *C. korshinskii* forest at restoration period of 40 a also comprised 9 plant seeds from 4 families and 9 genera, with a high total density of 7098.75 seeds/m^2. Similarly, *C. virgata* (45.92%), *E. minor* (40.10%), and *E. gmelinii* (6.29%) had the top three importance values for specific ecosystem in this environment. The soil seed bank of artificial *C. korshinskii* forest at restoration period of 20 a comprised 11 plant species across 4 families and 11 genera, with the overall seed density being approximately 3851.25 seeds/m^2. Among these species in the 20 a restoration forest sampling plots, *E. minor* had the highest important value (48.91%), followed by *C. virgata* (34.66%) and *E. gmelini* (4.84%).

3.4 Temporal dynamics of soil seed bank

The temporal patterns of soil seed bank exhibited a distinct bimodal distribution (Fig. 3). The initial peak value of soil seed bank density occurred on 10 July 2021, for both 40 and 20 a restoration period sampling plots, with densities of 2083.33 and 791.67 seeds/m^2, respectively; while for 60 a restoration period sampling plots, the initial peak value of soil seed bank density (1141.67 seeds/m^2) appeared on 10 August 2021. Subsequently, a decline occurred until 10 September 2021, then soil seed bank density started to rebound. By 10 November 2021, the end of the sampling period, 60 a restoration period sampling plots reached the highest density (2450.00 seeds/m^2), followed by 40 a (2208.33 seeds/m^2) and 20 a (1750 seeds/m^2) sampling plots.

Table 4 Composition of soil seed bank of artificial *C. korshinskii* forest at different restoration periods

Species	Family	Genus	Life form	60 a		40 a		20 a	
				Seed density (seeds/m^2)	Importance value (%)	Seed density (seeds/m^2)	Importance value (%)	Seed density (seeds/m^2)	Importance value (%)
E. minor	Poaceae	*Eragrostis*	Annual herb	2082.5±195.58^b	47.41	2846.25±196.16^a	40.10	1883.75±205.03^b	48.91
C. virgata	Poaceae	*Chloris*	Annual herb	1515.00±112.44^b	34.49	3260.00±249.90^a	45.92	1335.00±106.63^b	34.66
E. gmelinii	Compositae	*Echinops*	Annual herb	340.00±41.77^a	7.74	446.25±62.02^a	6.29	186.25±40.78^b	4.84
B. dasyphylla	Chenopodiaceae	*Bassia*	Annual herb	143.75±20.59^a	3.27	148.75±22.90^a	2.10	93.75±16.90^a	2.43
S. viridis	Poaceae	*Setaria*	Annual herb	111.25±22.17^a	2.53	152.5±34.60^a	2.15	81.25±16.31^a	2.11
S. collina	Chenopodiaceae	*Salsala*	Annual herb	95.00±19.75^b	2.16	182.5±32.65^a	2.57	156.25±32.29^{ab}	4.06
A. mongolicum	Poaceae	*Agropyron*	Perennial herb	50.00±14.40^{ab}	1.14	31.25±12.15^a	0.44	55.00±11.12^a	1.43
C. korshinskii	Leguminosae	*Caragana*	Shrub	33.75±12.20^a	0.77	12.50±8.98^a	0.18	12.50±6.41^a	0.32
A. squarrosum	Chenopodiaceae	*Agriophyllum*	Annual herb	21.25±11.51^{ab}	0.48	-	-	33.75±9.98^a	0.88
I. dentatum	Compositae	*Ixeridium*	Perennial herb	-	-	18.75±9.05^a	0.26	-	-
Corispermum mongolicum	Chenopodiaceae	*Corispermum*	Annual herb	-	-	-	-	7.50±5.47^a	0.19
A. desertorum	Chenopodiaceae	*Artemisia*	Perennial herb	-	-	-	-	6.25±4.00^a	0.16
	Total			4392.50±286.64^b	100.00	7098.75±444.28^a	100.00	3851.25±334.16^b	100.00

Note: Different lowercase letters for the same species indicate significant differences among different restoration periods at $P<0.05$ level. "-" means no data.

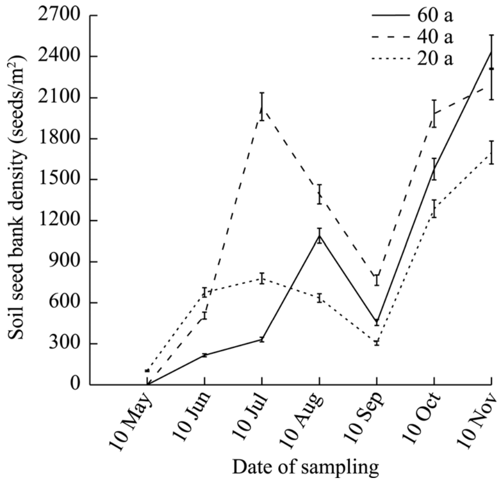

Fig. 3 Temporal dynamics of soil seed bank density of artificial *C. korshinskii* forest at different restoration periods. Bars are standard errors.

3.5 Vertical distribution of soil seed bank

In this study, we investigated the seed bank density at different soil depths of artificial *C. korshinskii* forest at restoration periods of 20, 40, and 60 a. As shown in Figure 4, seeds primarily concentrated within 0.0–2.0 cm topsoil layer at all the three restoration periods. As the soil depth increased, seed bank density gradually decreased, reaching a minimal or even zero distribution within 10.0–20.0 cm soil layer. While the substantial difference of seed density between the topsoil layer (0.0–2.0 cm) and the deep soil layers (2.0–5.0, 5.0–10.0, and 10.0–20.0 cm) gradually increased over time; the difference of seed bank density among the different soil layers was the smallest within the sampling plots at 20 a restoration period. The seed bank density in the 0.0–2.0 and 2.0–5.0 cm soil layers changed greatly under different restoration periods, but the seed bank density in the soil layers below 5.0 cm depth changed little under different restoration periods.

3.6 Relationship between seed rain and soil seed bank

The coefficient of similarity between seed rain and soil seed bank was calculated using the Sorensen formula. The species richness of seed rain in artificial *C. korshinskii* forest increased over time. The number of species in soil seed bank of artificial *C. korshinskii* forest at 20 a restoration period was the highest (11 species), while there was no difference between the sampling plots at 40 and 60 a restoration period. The coefficient of similarity indicated that the sampling plots at 20 a restoration period (85.71%) had higher similarity than the sampling plots at 40 (72.73%) and 60 a (69.57%) restoration periods (Table 5).

A positive correlation was observed between seed rain and soil seed bank at all the three restoration periods (Fig. 5). The regression slope of seed rain and soil seed bank decreased gradually with the increase of restoration periods, indicating that the growth rate of seed rain density was greater than that of soil seed bank density. In other words, with the restoration of ecological environment, species richness in seed rain increased significantly, while species richness in soil seed bank decreased (Table 5).

3.7 Species similarity among seed rain, soil seed bank, and aboveground vegetation

The species belonging to seed rain, soil seed bank, and aboveground vegetation were investigated and analyzed, and the coefficient of similarity was calculated (Tables 6 and 7). The results showed that the species similarity between soil seed bank and aboveground vegetation was higher than that between soil rain and aboveground vegetation. As restoration period increased, the species similarity decreased.

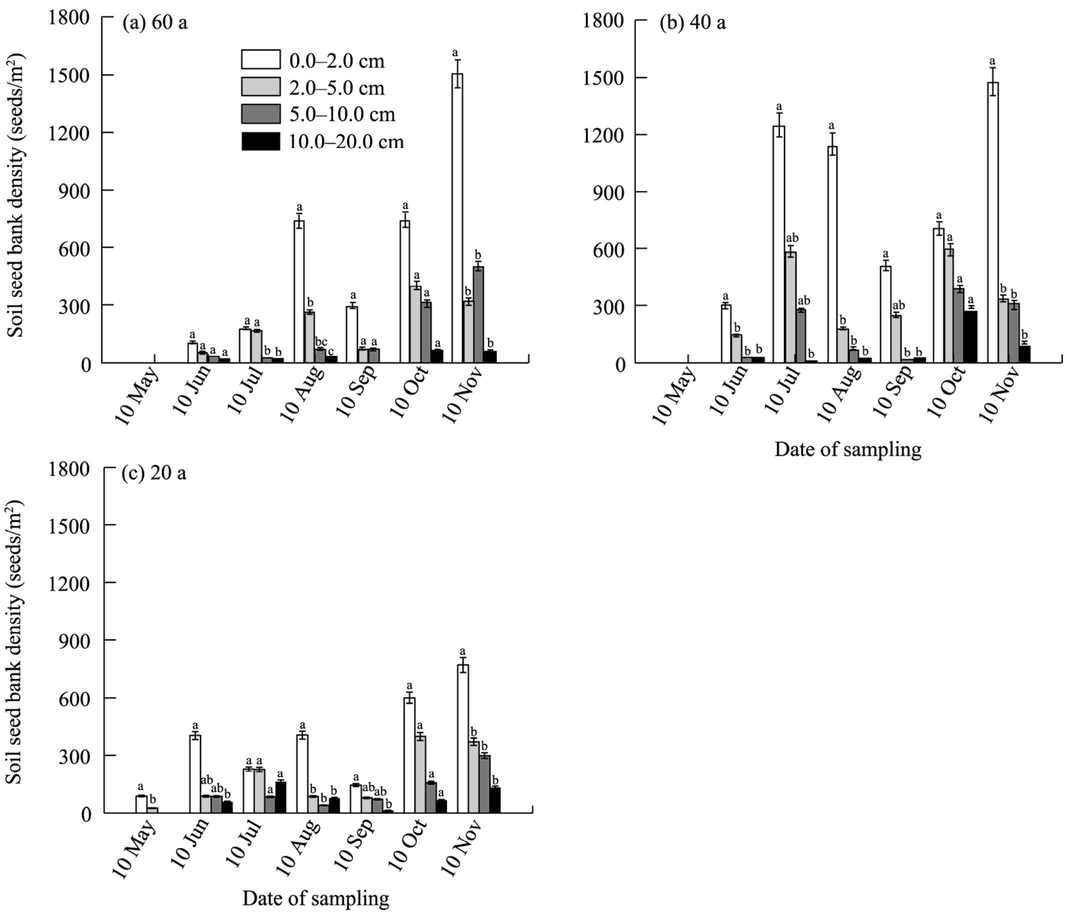

Fig. 4 Vertical distribution of soil seed bank density of artificial *C. korshinskii* forest at restoration periods of 60 (a), 40 (b), and 20 a (c). Bars are standard errors. Different lowercase letters indicate significant difference of soil seed bank density among different soil layers at $P<0.05$ level.

Table 5 Species similarity between seed rain and seed bank in artificial *C. korshinskii* forest at different restoration periods

Restoration period	Number of species in seed rain	Number of species in soil seed bank	Total number of common species	Coefficient of similarity (%)
60 a	14	9	8	69.57
40 a	13	9	8	72.73
20 a	10	11	9	85.71

4 Discussion

4.1 Temporal variation of seed density in seed rain and soil seed bank

In desert ecosystems, particularly in areas with artificial vegetation, seed rain and soil seed bank play crucial roles in the restoration and reconstruction of aboveground vegetation (Chen et al., 2017). Souza de Paula et al. (2023) showed that the Caatinga Dry Forest had relatively low density and poor seed rain and soil seed bank. In addition, in their study, seed rain and soil seed bank did not show directional changes through forest regeneration in most attributes and had little difference in scores from original stands, which is similar to the results of this study. Seed rain and soil seed banks are influenced by the species composition of aboveground vegetation. In this study, the similarity (86.96%) between seed rain and aboveground vegetation was remarkably high, whereas that between the soil seed bank and aboveground vegetation reached 95.24%. This observation could be attributed to the following factors. First, in arid and semi-arid areas, one of the main ways of plant community reproduction is to increase the seed setting rate, and a larger seed setting rate can increase the probability of seed occurrence (Siewert and Tielbörger, 2010). Second, limited plant height restricted the distance of seed dispersal (Tang et al., 2021).

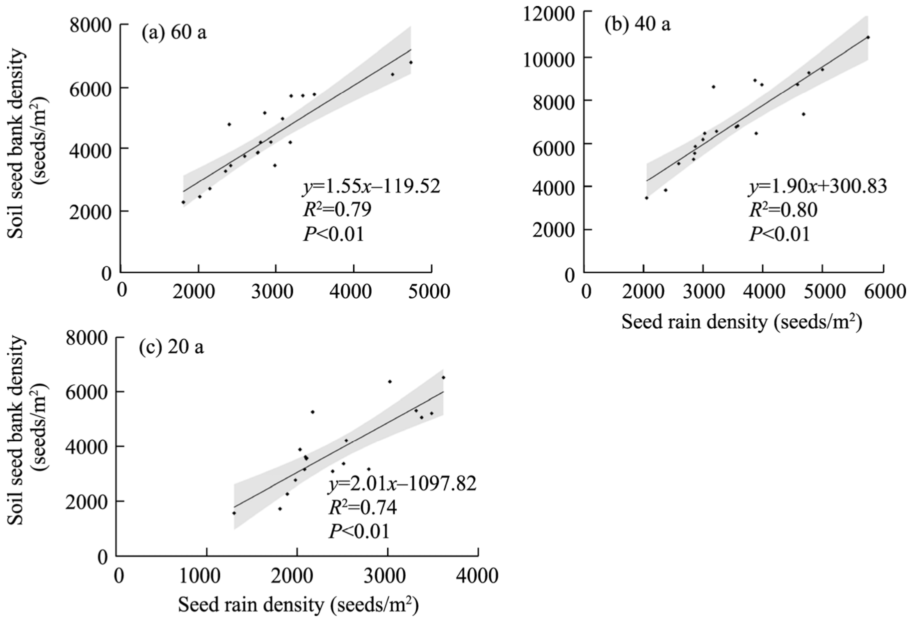

Fig. 5 Relationship between seed rain and soil seed bank in artificial *C. korshinskii* forest at restoration periods of 60 (a), 40 (b), and 20 a (c). The dark gray band is the 95% confidence interval of the regression.

Table 6 Species similarity between seed rain and aboveground vegetation in artificial *C. korshinskii* forest at different restoration periods

Restoration period	Number of species in seed rain	Number of species of aboveground vegetation	Total number of common species	Coefficient of similarity (%)
60 a	14	11	9	72.00
40 a	13	10	10	86.96
20 a	10	10	8	80.00

Table 7 Species similarity between soil seed bank and aboveground vegetation in artificial *C. korshinskii* forest at different restoration periods

Restoration period	Number of species in soil seed bank	Number of species of aboveground vegetation	Total number of common species	Coefficient of similarity (%)
60 a	9	11	8	80.00
40 a	9	10	9	94.73
20 a	11	10	10	95.24

Xu et al. (2012) showed that seed rain density and species richness are basically synchronized within ten years and both showed significant periodic fluctuations. Yu et al. (2015) believed that seed rain has high spatial and temporal heterogeneity due to rainfall and microtopography. Cai et al. (2019) showed that seed rain is affected by vegetation types and locations, and the species diversity of seed rain may differ from aboveground. Exotic species that did not exist in aboveground vegetation appeared in seed rain may have spread over long distances (Cai et al., 2019). Previous studies have also demonstrated the variations of temporal dynamic of seed rain in different plant communities. In this study, by observing the phenological periods of aboveground vegetation combined with the rainfall data in 2021, we found that the seeds of certain annual herbaceous plants (primarily *E. gmelinii*, but also *E. minor*) initiated germination after several rainfall events from late March to early June, then entered a period of full flowering from late June to July. Subsequently, fruiting commenced in July and continued until August when seed dispersal occurred, and this process concluded in early September. This completed the growth cycle and marked the formation of an initial peak in seed rain density. The second round of precipitation occurred in the study area between mid-August and early September. Annual herbs such as *C. virgata*, *Corispermum mongolicum*, and *S. collina*, along with Perennial plant *A. mongolicum*, entered their flowering phase during this period (Li et al., 2004), and seeds began to mature and scatter by early October. A "double peak" pattern for seed rain was, therefore, observed in this experiment. Notably, because of the similar vegetation composition among the artificial *C. korshinskii* forests at different restoration periods, consistent starting points, peaks, vanishing nodes, and durations were observed for the temporal distribution of seed rain.

Rainfall is the primary limiting factor in seed germination (Hogenbirk and Wein, 1992). Clauss and Venable (2000) demonstrated that rainfall significantly affects the seed germination of soil seed bank in desert areas. The soil particles in the study area mainly comprise fine sand with high water permeability, allowing easy infiltration of rainfall and providing favorable conditions for seed germination (Li et al., 2018). By considering the influence of rainfall on seed germination, we observed the response of seed germination in soil seed bank, which explains the occurrence of a "double peak" pattern in temporal dynamics of soil seed bank. After substantial rainfall in April, a considerable number of seeds sprouted from soil seed bank, leading to a low seed density by May. Subsequently, numerous seeds of annual herbs initiated growth, flowering, and fruiting after rainfall events and began dispersing seeds in early June. This occurrence led to a significant influx of seeds into soil seed bank, forming the first observed density peak in July. The second episode of heavy rainfall within the study area stimulated extensive germination of numerous seeds, which, subsequently, caused a sharp decline in soil seed bank density. From September to October, as seeds from second plants started spreading outward, they contributed substantially to replenishing the existing soil stockpile through importation into their respective forests (Muñoz-Rojas et al., 2016). A second peak in the overall seed density was established in this way.

4.2 Analysis of species richness changes in seed rain and soil seed bank

Several studies have indicated that seed morphology, including shape and appendages such as awns, spines, and crown hairs, could influence seed dispersal and the incorporation of seeds into soil seed bank (Thompson et al., 2014). For instance, although the seeds of *E. gmelinii* were the most abundant in artificial *C. korshinskii* forest, they did not dominate the soil seed bank. This phenomenon is ascribed to their achenes with dense and long yellowish-brown hairs that enable them to disperse over long distances in arid and semi-arid areas with strong winds (de Heredia et al., 2015). However, most of these seeds were intercepted by other herbaceous plants or shrubs during dispersal, making it difficult for them to settle in soil seed banks through natural settlement processes (de Andrés et al., 2014). Consequently, the seed density of *E. gmelinii* present in soil seed bank remained limited. In contrast, *B. dasyphylla* populations exhibited clustered distribution pattern horizontally because of relatively heavy seeds that have a smaller dispersal range but would more likely be captured by collectors designed. Despite fewer seeds of *B. dasyphylla* being observed in the overall seed rain and soil seed bank samples compared with *E. gmelinii*, *B. dasyphylla* showed higher abundance in soil seed bank because of their ability to settle effectively, along with the sedimentation processes facilitated by their weight. Grass species, such as *E. minor* and *S. viridis*, possess inherent advantages in terms of height and reproductive strategies, which confer absolute advantages to their population persistence (Zhang and Zhao, 2015). These grasses contributed significantly toward total seed rain and maintained substantial representations within soil seed bank (Chauhan and Johnson, 2010).

After recovery, the similarity between seed rain and soil seed bank gradually diminished over time (Table 6), which is ascribed to two factors. First, soils with longer restoration periods provide more favorable conditions for vegetation growth, resulting in a greater species composition of both vegetation and seed rain. Second, the presence of a soil biological crust hinders certain seeds with appendages from entering soil seed bank because they are dispersed over long distances. Additionally, in our samples, seeds that formed a relatively low proportion of seed rain, were susceptible to predation by birds, mice, and insects, leading to lower species numbers in soil seed bank (Janzen, 1971).

Owing to strong winds and sand in the study area, we positioned the seed rain collector 1.0 cm above ground level to mitigate potential wind and sand intrusion. There are some shortages in the study. First, this study focused solely on primary seed dispersal mechanisms (wind or gravity dispersal) and neglected the secondary dispersal processes (animal dispersal). Second, this study did not examine the interannual dynamics of seed rain and soil seed bank of artificial *C. korshinskii* forest. There are some advises for future research. Given the high sensitivity of seeds to rainfall in soil seed banks, namely, a substantial number of seeds germinated rapidly following rainfall events, if air seeding is employed for ecological restoration, it should be conducted during or one week before the rainy season (Li et al., 2016). Native species should be selected carefully as seed candidates, and gravity-based seeding methods should be prioritized to enhance the likelihood of seed incorporation into soil seed bank (Prasse and Bornkamm, 2000).

5 Conclusions

By systematically examining the species composition of seed rain and soil seed bank of artificial *C. korshinskii* forest at various restoration periods (60, 40, and 20 a) in the Tengger Desert, this study investigated the correlation between different sand fixation durations and species composition in seed rain and soil seed bank within the artificial *C. korshinskii* forest. The results showed that *E. gmelinii*. *E. minor*, and *A. mongolicum* had the highest seed rain density, while *E. minor*, *C. virgate*, and *E. gmelinii* had the highest soil seed bank density. As restoration period increased, the species richness gradually increased in seed rain and decreased in soil seed bank, but the seed density increased first and then decreased both in seed rain and soil seed bank. With the increase of restoration period, the species similarity between seed rain or soil seed bank and aboveground vegetation decreased gradually. There was a positive correlation between seed rain density and soil seed bank density among all the three restoration periods.

Conflict of interest

The authors declare that they have no competing financial interests or personal relationships that could influence the work reported in this study.

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Author contributions

Conceptualization: SHEN Jianxiang; Data analysis: WANG Xin; Methodology: SHEN Jianxiang, WANG Lei; Investigation: QU Wenjie, ZHANG Xue, YANG Xingguo, CHEN Lin; Situation analysis: WANG Lei, CHANG Xuanxuan, QIN Weichun, ZHANG Bo, NIU Jinshuai; Writing - original manuscript preparation: SHEN Jianxiang; Written and edited: WANG Lei, SHEN Jianxiang; Financing acquisition: WANG Lei; Resources: WANG Jiahui; Supervisor: ZHANG Xue; Project Management: WANG Lei; Software: SHEN Jianxiang; Authenticator: WANG Xin; Visualization: SHEN Jianxiang. All authors approved the manuscript.

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