



Properties and Distribution of Seed Banks in a Black Locust (*Robinia pseudoacacia*) Plantation in Central China

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ABSTRACT

We aimed to compare the properties of seed banks in different types of *Robinia pseudoacacia* stands and different substratum layers. We established four Black locust plots (each 50 × 50 m) that included two second-generation stands and two third-generation stands. Spatial coordinates, diameter at breast height, and the heights of all trees were measured in the four plots. In each plot, we set a total of 259 points using the regular grid design method. At these points, we sampled the seed banks in the litter and soil (0-5 cm) layers. The coordinates of the 259 points were recorded. After the samples had been collected and screened, a germination trial was performed using the collected seeds from the different layers and stands. We used variogram and kriging interpolation geostatistical methods to analyze the distribution of the seed banks. A kernel density estimation map was generated to examine the relationship between the seed bank and trees in each stand. The results showed that seed bank density was high in the four stands (4005-7325 seeds.m⁻²), and was higher in the third-generation stands (6085 and 7325 seeds.m⁻²) than in the second-generation stands (4005 and 5659 seeds.m⁻²). The seed bank density in the litter layer (3225 seeds.m⁻²) exceeded that in the soil layer (2164 seeds.m⁻²). The spatial pattern of the seed banks varied among different stands and was positively correlated with the distribution of trees in each stand. Furthermore, we found that spatial autocorrelation in the seed banks occurred at a variety of scales. Seeds in the litter layer were significantly more active than those in the soil layer; the germination rate varied from 6.67% to 28.89%. The findings of this study suggest that the *Robinia pseudoacacia* plantation in the Luoning area may exhibit potential for regeneration from seeds, and this will be the focus of our future studies.

INTRODUCTION

Seed banks provide important information on vegetation composition and dynamics, and they play critical roles in forest regeneration (Bigwood & Inouye 1988, Hille Ris Lambers et al. 2005, Skowronek et al. 2014), and are thought to represent potential plant communities within ecosystems (Hu et al. 2013). Both biotic and abiotic environmental factors affect the size, distribution, and species composition of seed banks in forests and other ecosystems. The total seed density within a seed bank is mainly influenced by stand age in natural forests (Bossuyt et al. 2002). When tree species are pollinated by insects, such as the honeybee, seed bank size is influenced by the extent of apicultural practice (Masaka et al. 2010). Investigations have shown that seeds in the bank are concentrated in the leaf litter, humus, and shallow soil depths (0–2 cm). The highest seed bank species richness is typically found in the 0–10-cm soil depth layer (Du et al. 2007, Cseresnyés & Csontos 2012, Hu et al. 2013, Douh et al. 2018).

Most of the studies about seed banks have focused on natural and mixed forests. However, seed banks are also important in the development and regeneration of pure artificial forests, especially in degraded multi-generation stands, but the compositional characteristics and spatial patterns of seed banks in such forests have rarely been studied directly. Black locust (*Robinia pseudoacacia*) is a native tree of North America. And the species was introduced to Luoning (Henan Province, China) from North Korea and planted widely in local hilly locations (Zhang et al. 2019). Natural regeneration in this area depends on root sucker production and stump sprouting after clear-cutting for timber production. However, stand growth has declined due to excessive asexual reproduction following several generations of rotation. Masaka et al. (2010) found that the density of black locust seeds in banks varied from 6.4 to 13757 seeds.m⁻² depending on honeybee pollination effectiveness and the basal area of the stands.

The characteristics of seed banks and seed germination need to be further studied in black locust plantations. To determine the spatial distribution of seed banks, large and small quadrat samples were collected for improved resolution and precision in predicting spatial patterns (Bigwood & Inouye 1988). Geostatistics is a suite of tools used to analyze regional variables based on variograms and kriging interpolation. We used kernel density estimation to analyze the spatial patterns in stands to assess the relationship between the seed banks and the aboveground trees in a black locust plantation. Our objective was to investigate (1) the density of the seed banks in the soil and litter layers, (2) the spatial patterns of the seed banks, (3) the relationship between each seed bank and the aboveground tree stand, and (4) seed germination capacity.

MATERIALS AND METHODS

Site Description and Experimental Design

The study area was located in Henan Province in central China. The site we chose is part of a government-owned forest farm. The climate is a warm temperate continental monsoon climate with an average annual temperature of 13.7°C (min. -21°C and max. 42°C), and the flora of this area belongs to the Chinese–Japanese plant sub-region of the Pan-Arctic plant region (Zhang et al. 2019). We selected four

experimental sites (Fig. 1) containing *R. pseudoacacia* stands in May 2017. The sites included two second-generation stands and two third-generation stands, which experienced once and twice clear-cutting respectively. For convenience, we used the abbreviations II-25, II-30, III-10, and III-17 as codes for the different stands. Codes II-25 and II-30 refer to second-generation stands that had been first clear cut 25 and 30 years previously, respectively. Codes III-10 and III-17 refer to third-generation stands, clear cut a second time 10 and 17 years previously, respectively.

A 50 × 50 m plot was established at each study site to investigate forest growth and seed bank properties. Basic information on the four plots is listed in Table 1. And 259 sampling points were selected at different scales in each plot (Fig. 2a) using a regular grid design procedure. At each sampling point, we set a 10 × 10 cm quadrat in which surface litter was collected. We collected a soil sample from the center of each of these quadrants. Cylindrical soil samples (5 cm radius, 5 cm depth) were collected using a soil ring knife (Fig. 2b). We then counted the number of seeds in the litter layer at each sampling position. The soil samples were sieved to separate the soil and seeds. Eight types of seed banks were categorized according to three factors: stand generation, stand age, and seed bank substratum (litter or soil), i.e., II-25-L, II-25-S, II-30-L, II-30-S, III-10-L, III-10-S, III-17-L, II-17-S.

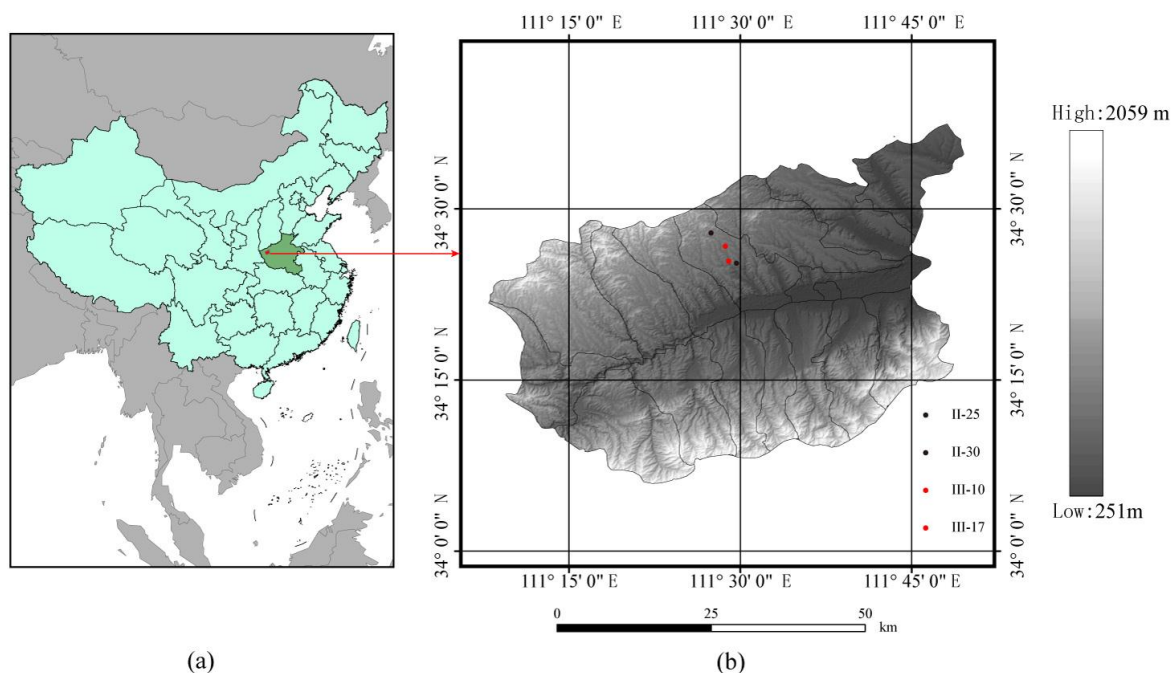


Fig. 1: (a) Location of the study area in China. (b) The distribution of the four plots (colored circles) overlain on a topographic map of the study area.

Table 1: Summary data for the four study plots.

Plot no.	Frequency of clear cutting	Age of stand (years)	Density of stand – [stems.ha ⁻¹]	Average DBH [cm]	Average height [m]	Tending after tree felling	Apicultural utilization	Slope aspect
II-25	1	25	1660	12.57 ± 4.47	9.83 ± 2.56	Yes	Yes	N-E
II-30	1	30	1224	14.00 ± 4.96	10.43 ± 2.64	Yes	Yes	E
III-10	2	10	5976	5.19 ± 1.64	6.85 ± 1.46	No	Yes	Flat
III-17	2	17	4056	6.84 ± 1.94	7.52 ± 2.38	No	Yes	W

Note: DBH, tree diameter at breast height

Germination Tests

We performed germination tests in the laboratory without physical or chemical interference to determine the germinability of Black locust seeds from different substrata and different stand types under natural conditions. Seeds of each seed bank type in each sample were mixed. We then randomly selected three replicates of 30 seeds from the litter and soil layers in each plot. In total, we selected 720 seeds from eight seed bank types for the germination experiment. The seeds were rinsed with distilled water before sowing. We sowed seeds in 24 flat nursery trays containing a mixture of nutritional soil and perlite in a 3:1 ratio. Trays were held at room temperature (20-25°C). Water was supplied daily for 30 days. The numbers of germinated seeds were counted daily at each census.

Data Analysis

Spatial Dependencies of the Soil Seed Banks

We chose geostatistical analysis, which is the best-known tool for assessing spatial autocorrelation (Matheron 1963, Wang 1999), to better understand the spatial characteristics of the seed banks of Black locust in an artificial pure forest, semivariograms to assess random and structural elements in soil seed bank distribution. The procedure defines the variance of an increment [$Z_{x+h} - Z_x$] over distance h and is expressed as follows:

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} (Z_{x+h} - Z_x)^2 \quad \dots(1)$$

where h is the lag distance, $\gamma(h)$ is the semivariance at lag distance h , $N(h)$ is the number of sample pairs at lag distance

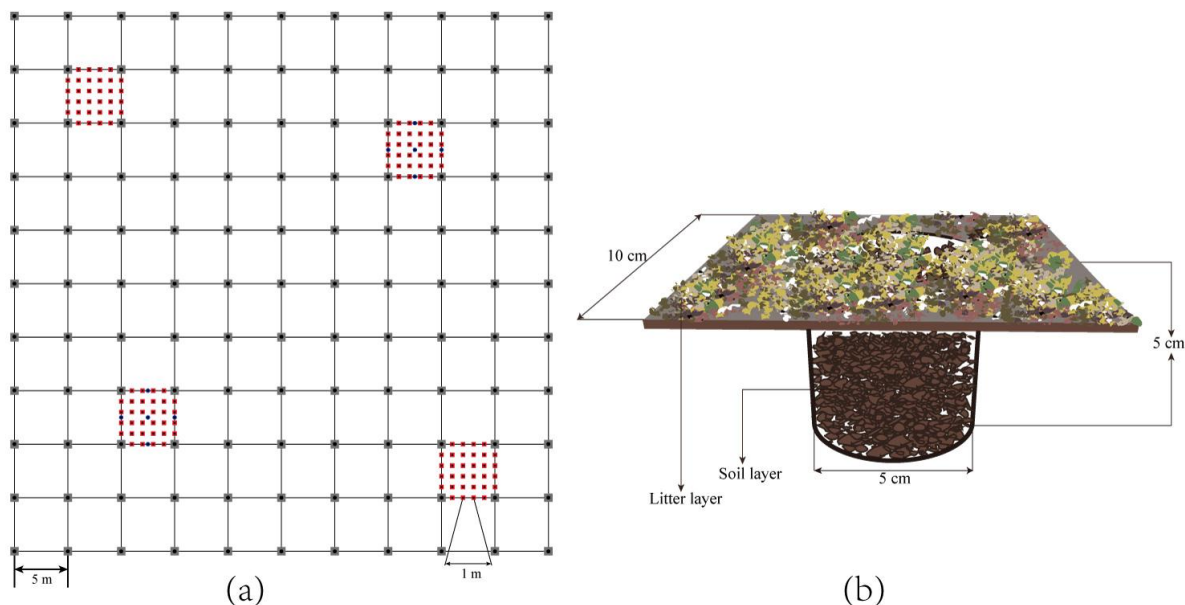


Fig. 2: (a) Distribution of 259 seed bank sampling points in each 50 × 50 m plot. (b) Schematic diagram of the litter- and soil-layer sampling at each point.

h , and Z_x and Z_{x+h} are the measured and observed values at point x and point $x+h$, respectively. A theoretical model can be used to fit the semivariance at different lag distances. This model will generate three characteristic parameters: nugget (C_0), sill ($C_0 + C$), and range (a), as shown in Fig. 3 for the spherical model.

The fractal dimension D is the slope of a log-log semivariogram plot (Orey 1970, Mandelbrot 1977, Burrough 1983) and reflects the complexity of information in a system (Ma & Zu 2000). We calculated fractal dimensions for the distributions of eight types of seed banks (according to generation, age, and substratum type). Semivariograms and fractal dimensions were calculated using GS+ software (Version 9.0, Gamma Design Software, Plainwell, MI, USA).

Kriging and Kernel Density Analysis

Kriging estimation is a procedure for “optimally predicting” points in space based on observations taken at known nearby locations (Cressie 1990). It offers an effective way of estimating a regionalized variable. Kriging was established by structural analysis of our semivariograms. The value of a point to be estimated is defined as follows:

$$Z_v^\#(x) = \sum_{i=1}^n \lambda_i Z(x_i) \quad \dots(2)$$

where λ_i is the weight coefficient of each point i around point v , and $Z(x_i)$ is the observed or measured value at the point i , and in this equation, $\sum_{i=1}^n \lambda_i = 1$.

To test the spatial relationship between the seed banks and stands, we used kernel density estimation to assess the spatial pattern of the stands. And we tested radii of 1, 2, 3, 4, and 5 m and the default search radius for each stand. We

selected 4 m as the most appropriate search radius in our study. Re-sampling was performed with bilinear interpolation after kernel density analysis to better display the density graph. Pixel sizes were set to 0.2×0.2 m in both kriging and kernel density analysis. We performed cell statistics and cell correlation analysis to examine the relationship between kriging and kernel estimation. All the analyses in this section were conducted using ArcMap 10.2 software (ESRI 2013).

Germination Analysis

Seeds were grouped into eight different categories (generation/age/substratum type). We assessed the influence on seed germination rate of (1) different stand ages, (2) the litter vs. soil layer, (3) different generations, and (4) seed bank category. The mean germination rate was subjected to multiple-comparisons tests or Student’s t-test ($p \leq 0.05$). We also analyzed the germination trend through the 30-day experimental period. All analyses were performed with the “multcomp” (Hothorn et al. 2008) and “ggplot2” (Hadley 2016, Team 2013) packages in R version 3.3.1 software.

RESULTS AND DISCUSSION

Results

Basic Characteristics of the Seed Banks

The density of seed bank (DSB) varied from 1762 to 4722 seeds.m⁻²; the maximum DSB occurred in the litter layer of the 17-year-old stand (III-17-L), and the minimum DSB occurred in the litter layer of the 30-year-old stand (II-30-L). The average variable coefficient of DSB in the second-generation stands (52.89%) was a little larger than that in the third-generation stands (50.32%) (Table 2). The DSBs in third-generation stands tended to be larger than those in second-generation stands (Fig. 4a). The DSB in the litter

Table 2: Statistical parameters for seed bank density (DSB) according to different generations, ages, and substratum types.

Type	n	Mean Density [seeds.m ⁻²]	Median Density [seeds.m ⁻²]	SD	CV [%]
II-25-L	259	3162	2800	2094	66.22
II-25-S	259	2497	2546	1284	51.42
II-30-L	259	1762	1700	764	43.35
II-30-S	259	2243	2037	1135	50.60
III-10-L	259	4267	3700	2533	59.36
III-10-S	259	1818	1527	925	50.88
III-17-L	259	4722	4700	2335	49.44
III-17-S	259	2603	2546	1091	41.91

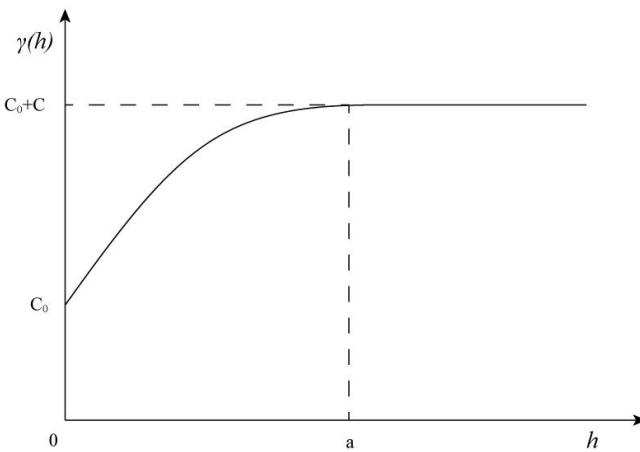


Fig. 3: The theoretical spherical semivariogram model. (h), semivariance at lag distance h ; $C_0 + C$, the sill parameter; C_0 , the nugget parameter; h , lag distance; a , range.

layer was larger than that in the soil layer (Fig. 4b), but not significantly so.

Spatial Autocorrelation in the Seed Banks

Most of the best-fitting variogram models were spherical models, though the exponential model fit well to II-25-L and II-25-S, and the Gaussian model fit well to II-30-L. Only the DSB variogram for stand II-25 had different model fits for the soil and litter layers. The spherical model provided the best fit for all DSB variograms for the third-generation stands (Fig. 5).

Variograms provided a measure of spatial variation in DSB with distance. Table 3 presents an overview of models and parameters for DSB variograms for each stand/layer type. All data were converted to normal distributions using square-root or log transformations, except the data for II-25-S and III-17-S. The range of spatial autocorrelation for the seed banks was 5.83–22.33 m. Spatial autocorrelation tended to be smaller in the soil layer than in the litter layer, except in stand II-25. The variance caused by spatial autocorrelation (defined as $C/[C+C_0]$) ranged from 50% for II-25-L to 75.8% for II-30-L. The spatial dependencies for all seed bank types (generation/age/substratum type) were $\geq 50\%$. The values of R^2 reflected a good fit (Table 3). The fractal dimension of the spatial pattern of DSB for all seed bank types was between 1.838 and 1.941, and the fractal dimension in the soil layer was a little larger than that in the litter layer, except in stand II-25. Overall, the fractal dimension (close to 2) revealed the complex spatial pattern of DSB (Table 3).

Spatial Relationship between Tree Stands and Seed Banks

Kernel density estimation of the stands and kriging interpolation in the DSB analysis showed that positive spatial relationships between the DSB and stand stem density existed

in all eight seed bank types (generation/age/substratum type) (Table 4). The maximum correlation coefficient (0.567) occurred in type III-17-L; the minimum value (0.432) occurred in type II-25-L. Spatial patterns of DSB in the litter and soil layers exhibited similar distribution trends (Fig. 6). DSB exhibited a decreasing trend with increasing stand age (Table 4). The kriging map showed that the DSB spatial pattern exhibited obvious patch characteristics, reflecting the

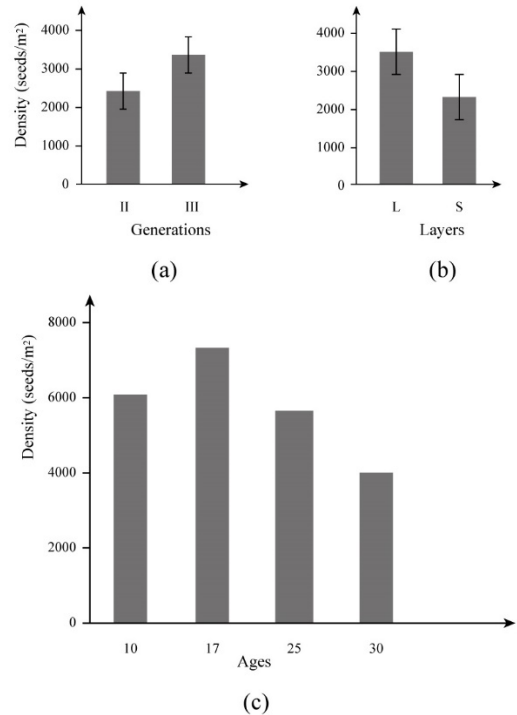


Fig. 4: Density of the seed bank (DSB) in second- and third-generation tree stands (a), different substratum types (b), and under trees of different ages (years) (c). II and III, generations 2 and 3, respectively; L, litter layer; S, soil layer.

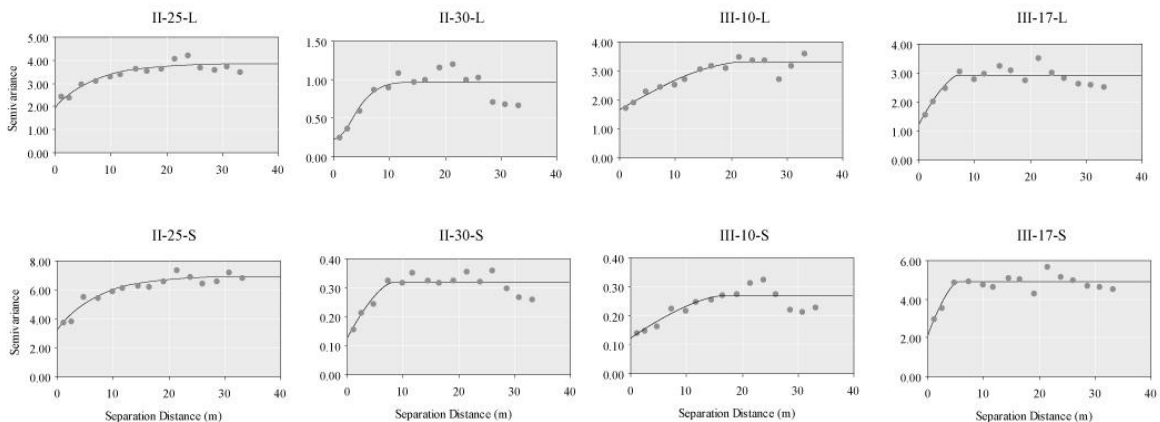


Fig. 5: DSB variograms for eight stand/layer types.

Table 3: Seed bank density (DSB) variogram parameters for each stand/layer type.

Type	Isotropic model	R ²	Still	Nugget	Range	C/C ₀ +C	Fractal dimension	Transformation
II-25-L	Exponential	0.849	3.837	1.918	19.92	50.00%	1.927 ± 0.236	Square-root transformation
II-25-S	Exponential	0.909	6.932	3.210	21.54	53.70%	1.907 ± 0.177	None
II-30-L	Gaussian	0.698	0.960	0.232	8.97	75.80%	1.838 ± 0.427	Square-root transformation
II-30-S	Spherical	0.754	0.321	0.126	8.83	60.80%	1.917 ± 0.466	Square-root transformation
III-10-L	Spherical	0.876	3.291	1.645	22.33	50.01%	1.899 ± 0.192	Square-root transformation
III-10-S	Spherical	0.703	0.268	0.122	17.33	54.50%	1.900 ± 0.382	Log transformation
III-17-L	Spherical	0.716	2.935	1.238	7.71	57.80%	1.930 ± 0.510	Square-root transformation
III-17-S	Spherical	0.763	4.913	2.149	5.83	56.25%	1.941 ± 0.469	None

Notes: Nugget and Still are characteristic parameters generated by the theoretical model fitting of the semivariance at different lag distances. C/C₀+C is the proportion of variation caused by spatial autocorrelation

heterogeneity of DSB. Patches of high value in the kriging map became larger with increases in high values of patches in the kernel density map for each stand generation. In summary, density and spatial distribution in the seed banks were positively influenced by tree distributions in stands within the *R. pseudoacacia* forest.

Germination Pattern During the Experimental Period

The trial showed that only a small proportion (<28.9%) of the seeds germinated during the study period. In the II-30-S

sample, only 6.67% ($\pm 2.72\%$) of the seeds germinated. In the t-tests and analysis of variance, there were no significant differences ($p > 0.05$) between second- and third-generation stands, and the rates did not differ significantly among stand ages. The germination rate of seeds from the third-generation stands was a little higher than that from the second-generation stands, but negligibly so (Fig. 7a). Germination rates were significantly different between the litter and soil layers ($t = 6.66$, $p < 0.01$); only 10% ($\pm 3.33\%$) of the seeds from the soil layer germinated (Fig. 7c). The germination rate of

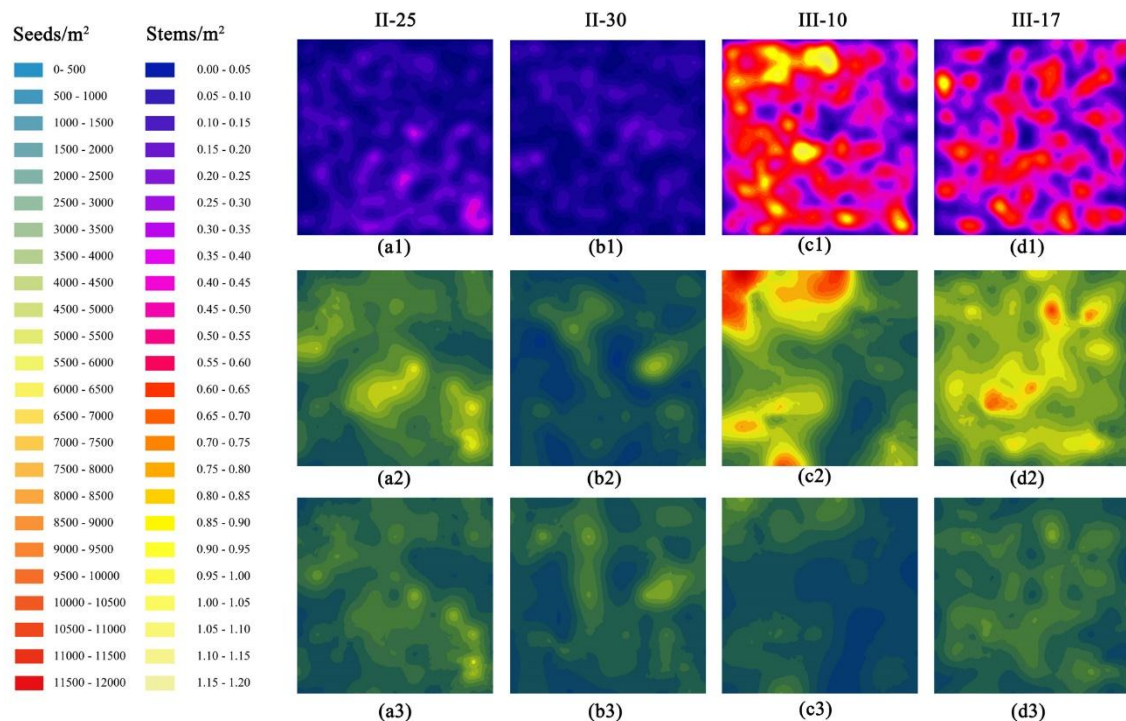


Fig. 6: Stand kernel density and kriging interpolation map of DSB. (a1), (b1), (c1) Kernel estimation map; (a2), (b2), (c2) kriging map of the seed bank in the litter layer; (a3), (b3), (c3) kriging map of the seed bank in the soil layer.

seeds differed significantly between the soil and litter layers in three stands, but not in stand III-10 (Fig. 7d). All seeds stopped germinating 19 days after sowing during the study period. Seeds from the litter layer began to germinate after 4 days, and the number of germinated seeds increased through 16 days. Germination occurred later in seeds from the soil layer and stopped after 19 days. The average number of days with germinating seeds for the litter layer (10 ± 1.87 days) exceeded the number of germination days for the soil layer (8.75 ± 3.56 days) (Fig. 8).

Discussion

Characteristics of the Seed Banks

The seed production of black locusts varies from year to year, and a good seed crop is generated approximately every 1–2 years after first flowering (Jastrzębowski et al. 2017). The DSB in stand III-17-L exceeded those in other stands, although the DSB in stand III-10-L was only slightly lower (Fig. 4). This DSB inequality among stands may be related to stand density, stand age, or seed production by mother trees. Stand development was shown to be an important factor influencing black locust DSB in Japan; stand biomass and apicultural activity can also be dominant determining

factors for the seed bank, rather than stand age (Masaka et al. 2010). The DSBs in four of our stand types were relatively high (4005–7325 seeds.m⁻²), far exceeding values in one previous report on DSB in forest soil (Silvertown & Charlesworth 2009). During the black locust flowering season, many beekeepers gather honey in the forests in our study area. This has a positive influence on seed production. Our seed bank sampling was conducted in May of 2017 because a large proportion of seed pods continue falling until April of the following year (Cierjacks et al. 2013), which may explain the DSB difference between the litter and soil layers.

Seed Bank Distribution

The spatial distribution of the seed bank is a function of dispersal processes related to the mother plants (Shaukat & Siddiqui 2004), as we demonstrated in our findings on the spatial relationship between the seed bank and stand (Table 4). The C/(C₀ + C) parameter in the variograms (Figs. 3, 5) represents the strength of spatial autocorrelation in the regional variable (Wang 1999). All structural variance ratios were >50%, indicating that the distribution of seeds in black locust stands depended more on biological processes than on random effects. We found strong autocorrelation in seed distribution at scales <9 m in the 25-year-old stand, which

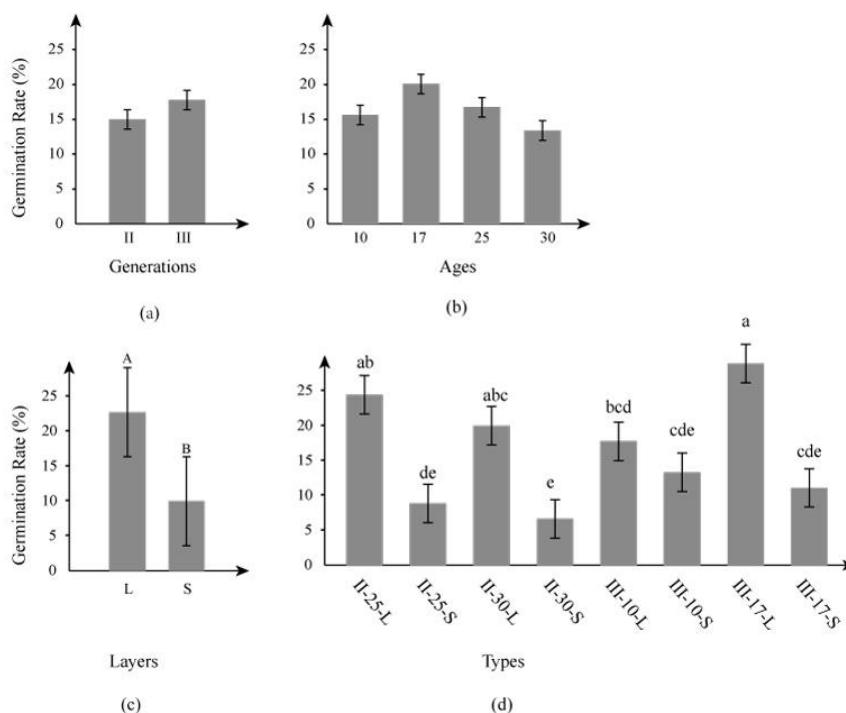


Fig. 7: Germination rates by tree generation (a), tree age (b), substratum type (litter vs. soil) (c), and seed bank type (generation/age/substratum type) (d). Each seed bank type was coded as follows: II and III, second and third generations, respectively; 10, 17, 25, and 30, stand ages in years; L and S, litter and soil, respectively. Different uppercase letters (A and B) in (c) indicate significant differences between layers (t-test, $p < 0.01$). Different lowercase letters in (d) identify significant pairwise differences between means ($p < 0.05$, Tukey's test).

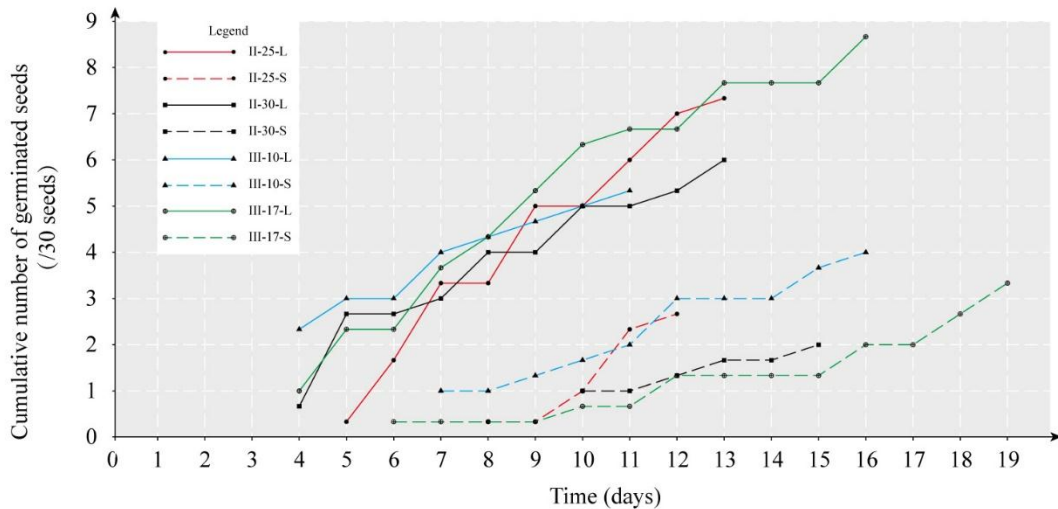


Fig. 8: Germination dynamics of seeds over 30 days in eight seed bank types (generation/age/substratum type).

was sparsely populated with trees. The sparseness of trees caused small patches in the kernel estimation (Fig. 6); consequently, the seeds were most aggregated at small scales.

Different models that fit variograms are representative of different types of spatial patterns in the field of geostatistics (Yavitt et al. 2009). Most of our variograms fitted well to spherical models, indicating the presence of distinct patches with high or low DSB, especially in the third-generation stands. We found a variety of best model fits for our variograms, suggesting that there is variation in the processes underlying the spatial patterns of seed banks.

Seed Germination According to Tree Generation, Tree Age and Substratum Type

The germination rate of black locust in nature is very low, as shown in many investigations (Masaka & Yamada 2009, Giuliani et al. 2015, Jastrzbowski et al. 2017) because the hard impermeable seed coat (Nicolescu et al. 2020), and no germinating seeds were found in the field during the season we surveyed. The germination rate of seeds from the litter layer significantly exceeded that of seeds from the soil layer (0-5 cm depth) (Fig. 7). Seeds from the litter also germinated earlier than seeds from soil (Fig. 8); hence, seeds in the litter layer were more active, suggesting that there may be varying degrees of seed dormancy in different layers of the black locust seed bank. Furthermore, seeds from our litter samples might have fallen in 2017, because we found that many seeds were still in the pods after collection.

Management Implications for Black Locust Plantations

The seed bank represents the regeneration potential of a forest

(Skowronek et al. 2014). The bank plays a major role in the restoration of degraded forest reserves and in maintaining ecosystem health (Taiwo et al. 2018). Seed germination under natural conditions is limited but can be improved greatly by scarification of the hard coat (Jastrzbowski et al. 2017). Furthermore, root suckers and stump shoots play important roles in the survival and spread of black locust stands (Carl et al. 2019). From a long-term forest management perspective, seedlings produced from seeds are healthier than new growth from root suckers, and root suckers produced far from the mother tree are healthier than stump shoots. An abundant seed bank provides great potential for sexual regeneration. We suggest that the frequencies of seedlings should be increased

Table 4: Statistics from kernel density estimation and kriging interpolation.

Kernel density or kriging map	Mean value of the pixel	SD	Correlation coefficient with stand
II-25 stand (A1)	0.158	0.073	–
II-25-L (A2)	3117.410	861.130	0.432
II-25-S (A3)	2493.640	570.340	0.496
II-30 stand (B1)	0.116	0.057	–
II-30-L (B2)	1697.090	652.680	0.512
II-30-S (B3)	2156.410	595.800	0.490
III-10 stand (C1)	0.4890	0.184	–
III-10-L (C2)	4110.740	1808.070	0.501
III-10-S (C3)	1751.790	604.210	0.497
III-17 stand (D1)	0.386	0.140	–
III-17-L (D2)	4561.310	926.300	0.567
III-17-S (D3)	2502.549	494.380	0.524

during tending and cutting. This will be an important focus in our future investigations.

CONCLUSION

The seed bank in forest soil and litter layers is essential and important for regeneration, but there are few specific studies on seed banks in artificial pure forests of Black locusts. Our study focused mainly on seed germination, and the properties and distribution of seed banks in four black locusts stand types in central China, and this study set out to explore the seed bank patterns and germination potential of multi-generation Black locust plantation. We found that seeds were abundant in the litter and soil layers, the DSBs (density of seed banks) in the third-generation stands exceeded those in the second-generation stands. What's more, we found spatial dependence at different scales in different types of seed banks and the large spatial structure ratio in the variograms indicated that the seed bank pattern was strongly influenced by autocorrelation. By fitting different semi-variance models, the results of this study suggest that spherical, exponential, and Gaussian models fit well to different variograms for the eight seed bank types (stratified by generation/age/substratum type). The germination rate varied with the substrate, the results have shown that seeds in the litter layer were more active than those in the soil layer. Based on these findings, our future investigations will consider the potential role of the seed bank in the regeneration of black locust plantations; we intend to create gaps in the forest and use artificial seed scarification to break dormancy, thereby increasing the proportion of seedlings in black locust forests.

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