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A spontaneous spread of black locust (*Robinia pseudoacacia* L.): the importance of seed and vegetative reproduction

Olga Kunakh[1], **Irina Ivanko**[1], **Kyrylo Holoborodko**[1], **Olexander Zhukov**[2*]

[1]Oles Honchar Dnipro National University, Gagarin av., 72, 49000, Dnipro, Ukraine
[2]Bogdan Khmelnitsky Melitopol State Pedagogical University, Hetmanska st., 20, 72318, Melitopol, Ukraine

Abstract

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The importance of seed and vegetative propagation for the spontaneous expansion of black locust on abandoned agricultural land was evaluated in the present study. The dynamics of expansion was reconstructed on the basis of spatial distribution data on the age of individuals of this species. A non-homogeneous Poisson process with a linear trend and a Widom-Rowlinson model were the most appropriate in explaining the spatial distribution of *R. pseudoacacia* individuals. The negative linear trend was statistically significant for the vast majority of polygons in the area of spontaneous expansion of *R. pseudoacacia*, but insignificant in the artificial plantation. The model parameter η indicates the aggregated spatial distribution of *R. pseudoacacia* in the zone of spontaneous spread due to the vegetative mechanism of spread. The distribution of *R. pseudoacacia* in the artificial tree plantation was close to regular, or either random or aggregated. In the early stages, the seed reproduction is the most likely process of *R. pseudoacacia* spreading. The seed mechanism of spreading follows a spatial pattern, which is explained by a linear trend. The next stage is a combination of both seed and vegetative mechanisms of spread, which also lasts about 4–5 years. At the last stage, the spread occurs mainly through the vegetative mechanism, and the rate of spread of the community slows down significantly. The trigger for the spread is anthropogenic impact.

Keywords

abandoned land, invasion, landscape, point analysis

Introduction

The North American species black locust (*Robinia pseudoacacia* L.) is currently the most widespread adventive tree species in Europe with a total area of its secondary range in the world about 2.3 × 10^6 ha (Nicolescu et al., 2020). The species is a drought-tolerant, fast-growing plant with a wide ecological amplitude with respect to soil conditions. Its plantations have a significant economic role in many countries performing a large number of essential ecosystem services: carbon sequestration, soil nitrogen enrichment, soil erosion protection, field protection functions, microclimate optimization, bioenergy and wood production (Nicolescu et al., 2020; Tutova et al., 2022). The increasing rate of black locust invasion as a thermophilic species in the natural forests of Central Europe is connected with climate change (Nadal-Sala et al., 2019). Climate change towards warming is believed to increase the presence of this species in the areas already colonized and to expand its current range. The black locust is resistant to an increased frequency of periodic droughts, which is one of the expected consequences of global climate change.

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*Corresponding author:
e-mail: zhukov_dnipro@ukr.net

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The successful naturalization of black locust in the secondary range and the high invasive potential of the species are determined by the fact that *R. pseudoacacia* is a habitat generalist which posses successful reproduction strategies (Puchałka et al., 2021). *R. pseudoacacia* is a pioneer in the primary range, but is not competitive enough. The species quickly colonizes destructive forest thinning areas, but in 15–30 years it is replaced by the other forest species. The black locust can actively compete with native species in the secondary range under conditions of natural or anthropogenic disturbance of the forest canopy (winds, tree fall, fire sites, cutting) disrupting the natural process of reforestation (Maringer et al., 2012). The spontaneous populations of *R. pseudoacacia* in the secondary range can exist for a long period of time, mainly because of the absence of natural enemies of the black locust outside its natural range. The reasons for extensive spontaneous spread of *R. pseudoacacia* in Europe and for its invasion to the different types of ecosystems are the regional peculiarities of forestry (Sádlo et al., 2017), associated with creation of a large number of areas of artificial plantations for various functional purposes (field protection, for reclamation of disturbed lands, for fixing ravines, for biomass production, etc.), which later become the sources of phytoinvasions (Holoborodko et al., 2022).

R. pseudoacacia is a light-demanding pioneer species which is able to spread rapidly outside the artificial plantations of the xeric-mesophytic habitats (Vítková and Kolbek, 2010). The *Robinia* prevails in the initial stages of forest regeneration (Radtke et al., 2013). It can spread rapidly over short distances. The long-distance spread is mostly dependent on human-related activities, such as deliberate planting and/or transportation of soil containing seeds and roots (Pyšek et al., 2012). The vegetative propagation strategies of *R. pseudoacacia* include the regrowth of stumps and root suckers (Carl et al., 2017). Disturbed habitats create suitable conditions for the spread of *R. pseudoacacia*, as well as the spread of accompanying weeds that have adapted evolutionarily to fill in the newly created gaps in the vegetation cover (Środek and Rahmonov, 2021). The large-scale disturbance of landscapes with consequent abandonment promotes the spontaneous succession of *R. pseudoacacia* (Jírová et al., 2012). The key reason for successful invasion of *Robinia* is its ability to spread rapidly through the spatial expansion of root shoots (Carl et al., 2019). The development of sprouts is a strategy for growth and expansion, as well as for adaptive response to damage (Jeník, 1994). Clonal dispersal plays an important role in the spread and success in competing for resources on the new territories (van Groenendael et al., 1996). This species quickly colonizes open areas in suburban wastelands, which is quite important for restoring vegetation cover in disturbed landscapes (Nicolescu et al., 2020). Fire-damaged areas with good light conditions are mostly colonized by the invasive *R. pseudoacacia*, whereas the vegetation cover from autochthonous species is restored mainly under shaded conditions (Maringer et al., 2012).

The *R. pseudoacacia* trees are spreading via seeds and root suckers (Vítková et al., 2017). However, the problem concerning the relationship between these two strategies of the *R. pseudoacacia* spontaneous expansion on the lands that have ceased to be used for agricultural production remains to be fully investigated. The present study aims in evaluation of expansion dynamic of the species to the abandoned agricultural lands based on the data on spatial distribution and age of *R. pseudoacacia* individuals in the community formed by spontaneous spread and to determine the contribution of seed and vegetative reproduction to the process.

Materials and methods

Location of the study

The study area is located on the right bank of the Dnipro River (Dnipro region, Ukraine, 48.26°N 35.17°E). The climate is continental, with an average annual temperature of 9.9 ± 0.2 °C (in the range of 8.4–12.4 °C) over the period 2000–2022 with an average annual temperature increase of 0.07 °C. The average annual precipitation was 555 ± 17 mm (in the range of 429–696 mm). The region's landscapes are dominated by broad, slightly undulating plains. Loess and loess-like loams are the most common geological surface rock, reaching a thickness of several tens of meters (Samoilych and Mokritskaia, 2016). The study area belongs to the Central Pontic steppe zone, which is rich in herbs (EuroVegMap https://www.synbiosys.alterra.nl/eurovegmap/). The natural vegetation is dominated by cereals and grasses. Soil is Calcic Chernozem (Siltic, Tonguic) (Yakovenko and Zhukov, 2021).

The trees were recorded and measured in the fall of 2022. The plant community subjected to study was formed as a result of spontaneous spread of *R. pseudoacacia* from the artificial forest plantation within abandoned agricultural field. The artificial tree plantation was established more than 50 years ago. At present, it surrounds the eastern corner of the field. In the southern part of the artificial tree plantation, a gully with natural steppe vegetation may be found. Since the end of the 20th century, the exploitation of the eastern part of the field has been stopped. At this time, the restoration of grass vegetation has begun, followed by a spontaneous spread of *R. pseudoacacia*. The plants reproduced prevailingly by sprouts. Seven experimental plots were located in the area of spontaneous spread of *R. pseudoacacia*. The start of the polygon (the beginning of the local coordinate system) was close to the artificial forest plantation, and the polygon itself (the direction of the abscissa axis of the local coordinate system) was directed towards spontaneous spread of *R. pseudoacacia* over time. A 90-meter-long measuring tape served as the abscissa axis relative to which the coordinates of tree trunks and shrubs were established at the ±3 meters distance. Thus, the area of each polygon was 0.054 hectares (540 m^2). The artificial tree plantation was represented by the field protection forest belt that was established 50 years ago. Four polygons of similar size were placed within the artificial tree plantation along the row direction.

Estimation of morphometric features of trees

Diameter at breast height (DBH) and diameter at root collar (DRC) were measured to the 0.1 cm precision, and the height (H) of all trees to the 0.01 m precision. The diameter and height were measured using an optical height meter (PM-5/1520 model; Suunto Instrument Co., Helsinki, Finland). The age of the plants was determined visually by an expert. In young individuals, the number of mutations was taken into account, in older trees, the attention was paid to their size. The age of the plants was clarified by the regression dependence of age on morphometric traits, based on a sample of plants for which the age was determined by annual rings (Kunakh et al., 2023). The plants are grouped by age into the following age classes: 1–2, 3–4, 5–14, 15–45 years and more than 50 years.

Statistical analysis

The descriptive statistics, linear regression analysis, and ANOVA were performed using software STATISTICA 12.0 (StatSoft Inc., 2014). The spatial distribution of trees was described using point pattern analysis in the *spatstat* library (Baddeley et al., 2013) for A language and environment for statistical computing *R* (R Core Team, 2020). The spatial segregation for several species was made by analyzing the nearest neighbour table counts for the pattern with marked points based on the Dixon index (Dixon, 2002) using the *dixon* library (De la Cruz, 2008). The spatial database was created in the ArcGIS 10.0 software (ESRI, 2011).

Results

There were 10 species of trees and shrubs within the spontaneous distribution of *R. pseudoacacia*, among which *R. pseudoacacia* makes up 88.4% by number of individuals (Table 1). The *R. pseudoacacia* over 14 years old were not found in the community in the area of spontaneous dispersal. The distribution of *R. pseudoacacia* individuals according to age classes in spontaneous colonization zone was unimodal asymmetric with an obvious predominance of plants aged 4 years (Fig. 1). The average age of individuals was 4.1 ± 0.05 years. The asymmetry of the age distribution was 1.3 ± 0.06, indicating a shift in the distribution to the left. The kurtosis was 3.0 ± 0.13, which indicates a significant predominance of the modal age stage, namely age 4 years. The plants aged 1–2 years accounted for 18.5% of the total number of *R. pseudoacacia*, plants aged 3–4 years accounted for 48.7%, and plants aged 5–14 years accounted for 32.8%.

There were 20 species of trees and shrubs in the artificial tree plantation. The *R. pseudoacacia* accounted for 52.3% of the total number of individuals in the community. The *Prunus spinosa* (14.1%) and *Cotinus coggygria*

Table 1. Species composition of artificial tree plantations and communities in the area of *Robinia pseudoacacia* spontaneous spread

Species	Spontaneous spread of the plantation							Artificial plantation			
	S1	S2	S3	S4	S5	S6	S7	A1	A2	A3	A4
Robinia pseudoacacia (Total)	156	248	198	188	189	201	336	113	98	93	89
1–2 year old	40	45	34	18	36	39	69	1	–	3	–
3–4 year old	56	100	104	102	96	89	191	1	2	13	3
5–14 year old	60	103	60	68	57	73	76	54	50	39	31
15–45 year old	–	–	–	–	–	–	–	34	27	20	33
50+ year old	–	–	–	–	–	–	–	23	19	18	22
Acer negundo	2	2	2	–	14	–	2	–	–	2	13
Acer platanoides	–	–	–	–	1	–	–	–	–	–	–
Acer tataricum	–	1	1	1	–	1	–	1	–	–	1
Amorpha fruticosa	–	–	–	–	–	–	–	–	–	–	3
Cotinus coggygria	–	–	–	–	–	–	–	29	25	46	5
Crataegus monogyna	–	–	–	–	–	–	–	16	2	1	10
Euonymus verrucosa	–	–	–	–	–	–	–	12	–	–	–
Fraxinus pennsylvanica	1	12	23	7	20	–	1	9	–	–	9
Juglans regia	–	–	–	–	–	–	–	2	–	1	–
Morus alba	–	–	–	–	–	–	–	2	1	–	–
Prunus armeniaca	–	–	–	–	–	–	–	1	–	–	1
Prunus mahaleb	–	–	–	–	–	–	–	–	–	1	–
Prunus spinosa	–	–	–	–	–	–	–	43	–	–	63
Pyrus communis	–	–	4	1	–	–	–	2	–	4	–
Quercus robur	–	–	–	–	–	–	1	1	16	1	1
Rhamnus cathartica	–	–	–	–	–	–	–	–	–	2	–
Rosa canina	–	–	–	–	–	–	–	–	–	1	–
Sambucus nigra	–	–	–	–	–	–	–	–	13	5	–
Ulmus laevis	–	–	–	–	–	1	–	–	–	–	–
Ulmus minor	4	1	3	73	9	2	1	8	–	–	–
Ulmus pumila	–	–	–	3	4	1	–	5	–	–	1

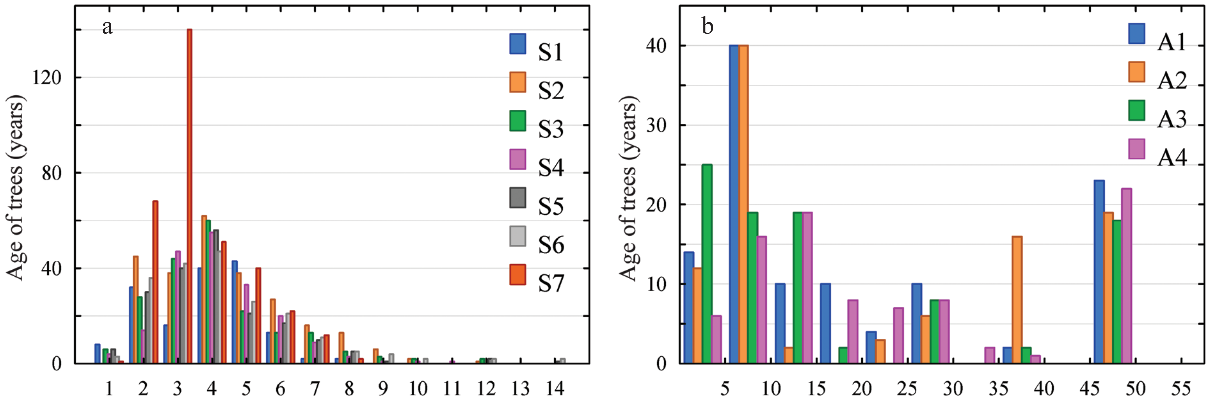

Fig. 1. Age structure of the *Robinia pseudoa*cacia population in the area of spontaneous dispersal (a) and in the area of artificial tree plantation (b). The abscissa is the age of individuals (in years); the ordinate is the number of individuals of the corresponding age.

(13.4%) also had an important role in the community. The age distribution of *R. pseudoacacia* individuals in the artificial plantation was represented by almost discrete age classes of 1–4, 5–10, 11–20, 21–30, 31–40 and 50 years. The *R. pseudoacacia* aged 50 years accounted for 20.9% of the total number of the individuals of this species (Table 1).

The parameters of the point process models were estimated based on the information on spatial distribution of *R. pseudoacacia* individuals. The spatial distribution of *R. pseudoacacia* populations differed significantly from the random alternative, which can be modeled by a Poisson process. The non-homogeneous Poisson process with linear trends and the Widom-Rowlinson model had the best ability to explain the spatial distribution of the point objects, which were considered to be *R. pseudoacacia* individuals. This is also confirmed by comparing the observed values of the *K*-function with the random alternative (Figs S1, S2). The negative coefficient for describing the linear trend was statistically significant for the vast majority of polygons in the area of spontaneous distribution of *R. pseudoacacia*, while in the artificial plantation the linear trend was not statistically significant (Table 1). The model parameter η indicates that in the area of spontaneous distribution, the spatial distribution of *R. pseudoacac*ia was aggregated due to the interaction between trees. The distribution in the artificial tree plantation was close to regular (polygons A1, A2), or random (A3) or aggregated (A4).

The negative linear trend in the area of spontaneous spread was the largest for plants aged 1–2 years (Planned comparison $F = 4.12$, $P = 0.05$) (Table 2). Other age groups of plants did not differ from each other by this indicator (Planned comparison $F = 1.72$, $P = 0.20$) and their linear trend was statistically significantly less than zero (Planned comparison $F = 7.38$, $P = 0.012$). The statistic η for plants aged 5–14 years was not statistically significantly different from 1 (Planned comparison $F = 0.78$, P = 0.38), while for younger plants this statistic was greater than one (Planned comparison $F = 44.6$, $P < 0.001$). The η statistic for plants aged 3–4 years was higher than that for plants aged 1–2 years (Planned comparison $F = 5.49$, $P = 0.028$). The linear trend has not differed significantly from zero for the sample within the artificial tree plantation ($F = 1.5$, P = 0.27) (Table 3). The η statistic was statistically significantly less than one for trees aged 50 years (Planned comparison $F = 34.4$, $P < 0.001$). This statistic for plants aged 5–14 and 15–45 years was not statistically significantly different from one (Planned comparison $F = 0.93$, $P = 0.35$).

The trees of age groups 1–2 and 3–4 years demonstrated mutual attraction in a zone of spontaneous distribution of *R. pseudoacacia* (Table 4). Trees of the age groups 1–2 and 3–4 years demonstrated repulsion from trees of the age group 5–14 years. The total number of statistically significant segregation coefficients in the artificial tree plantation was significantly lower than in the area of spontaneous spread. The *R. pseudoacacia* plants aged 5–14 and 15–45 years showed repulsion. The repulsion was also found for the interaction between *R. pseudoacacia* aged 50 years and *Cotinus coggygria*. The plants of *Fraxinus pennsylvanica*, *Cotinus coggygria*, and *Prunus spinosa* showed an aggregate distribution.

The analysis of the dynamics of emergence of *R. pseudoacacia* plants of different ages shows that the first plants in the area of spontaneous spread appeared at a considerable distance from the artificial tree plantation (Figs S3, S4). The calculations of the closest distance to individuals of older age stages indicate that the youngest plants were located at the smallest distance from older individuals, and this indicator increased with age (Fig. 2). The plants can be divided into three groups according to the absolute values of distances and their specific distribution (Fig. S5). The oldest group of plants aged 9–14 years was recognized by the large values of distances to the nearest older individuals and unimodal distribution of this indicator. The Kolmogorov-Smirnov test for the normal distribution of log-transformed distances was $d = 0.073$, $P = 0.98$. The kurtosis did not differ significantly from zero and was 0.17 ± 0.78. The plants of this age group were located at a distance of 10.6 ± 0.15 meters from the nearest older individual of the same species (95% percentile was in the range of 1.2–87.0 meters). The youngest group of plants aged 1–5 years had the smallest values of distances and also a unimodal distribution of this indicator. The youngest plants aged 1–2 years were on average at a distance of 0.63 ± 0.04 meters (95% percentile was in the range of

Table 2. Fitting of point process models to the observed point pattern of *Robinia pseudoacacia* distribution in the area of spontaneous spread

Polygon	Age class	Homogeneous Poisson process		Non-homogeneous Poisson process with a linear trend			Non-homogeneous Poisson process with linear trend and Widom-Rowlinson model				
		λ_1	AIC_1	λ_2	k_2	AIC_2	r	λ_3	k_3	η	AIC_3
S1	Total	0.24	759.74	0.41	–0.0128*	743.90	0.97	0.10	–0.0059*	2.30	327.37
	1–2	0.06	305.17	0.17	–0.0276*	288.27	0.42	0.15	–0.0237*	2.23	240.42
	3–4	0.09	388.75	0.23	–0.0266*	366.04	1.54	0.02	–0.0021	4.01	55.04
	5–14	0.09	408.10	0.07	0.0067	408.16	1.64	0.04	–0.0082	0.91	33.34
S2	Total	0.38	976.68	0.59	–0.0100*	961.19	0.62	0.16	–0.0048*	2.41	492.08
	1–2	0.07	332.47	0.15	–0.0191*	323.51	0.35	0.14	–0.0153*	2.82	292.74
	3–4	0.15	576.67	0.20	–0.0061	576.01	1.16	0.01	–0.0013	4.40	128.29
	5–14	0.16	587.82	0.24	–0.0101*	582.46	1.68	0.56	–0.0302	–0.16	37.13
S3	Total	0.30	869.34	0.45	–0.0093*	859.35	1.18	0.07	–0.0014*	2.30	231.88
	1–2	0.05	270.75	0.04	0.0035	272.45	1.68	0.08	–0.0157*	2.54	215.71
	3–4	0.16	591.50	0.22	–0.0069	589.92	1.68	0.05	–0.0323	2.92	28.42
	5–14	0.09	408.10	0.21	–0.0215*	391.97	1.69	0.14	–0.0290	0.72	25.02
S4	Total	0.29	845.02	0.37	–0.0059*	842.38	0.50	0.21	–0.0028*	1.78	562.85
	1–2	0.03	167.17	0.03	0.0006	169.17	1.02	0.01	–0.0117*	0.11	63.02
	3–4	0.16	584.12	0.14	0.0028	585.53	0.27	0.12	0.0041	2.29	510.31
	5–14	0.10	445.22	0.24	–0.0219*	425.88	1.68	0.00	0.0165	1.08	17.76
S5	Total	0.29	847.50	0.60	–0.0182*	807.43	0.20	0.38	–0.0107*	2.76	632.84
	1–2	0.06	282.44	0.22	–0.0412*	252.09	1.39	0.02	–0.0144*	2.31	31.65
	3–4	0.15	561.52	0.22	–0.0093*	557.67	0.32	0.19	0.0101	3.17	436.03
	5–14	0.09	393.64	0.21	–0.0224*	377.05	0.79	0.23	–0.0193*	1.02	207.99
S6	Total	0.31	876.43	0.67	–0.0197*	826.36	1.40	0.07	0.0034	1.97	172.39
	1–2	0.06	299.57	0.17	–0.0281*	282.62	0.57	0.11	–0.0296*	1.82	207.85
	3–4	0.14	534.20	0.31	–0.0212*	509.94	1.69	0.01	–0.0079	2.70	14.51
	5–14	0.11	467.46	0.20	–0.0141*	459.48	0.39	0.25	–0.0174*	0.32	370.77
S7	Total	0.52	1118.46	0.53	–0.0005	1,120.41	1.45	0.02	–0.0010	3.96	182.78
	1–2	0.11	449.73	0.11	–0.0003	451.72	1.69	0.01	–0.0234*	1.77	25.10
	3–4	0.29	852.42	0.31	–0.0014	854.15	0.25	0.32	–0.0008	1.25	792.96
	5–14	0.12	480.46	0.11	0.0017	482.30	0.31	0.11	0.0010	1.20	418.88

λ_1 is the intensity of the homogeneous Poisson process (trees m^{-2}), λ_2 and λ_3 are the free terms of the nonhomogeneous Poisson process model, k_2 and k_3 are the linear trends, r is the radius of the disks in the area interaction process, or the irregular parameter of the Widom-Rowlinson model found by maximizing the AIC criterion, η is the interaction parameter, which can be any positive number: If $\eta = 1$, then the model reduces to a Poisson process with intensity λ_3; if $\eta < 1$, then the process is regular, and if $\eta > 1$, then the process is clustered. Two points interact if the distance between them is less than $2r$. Asterisk (*) denotes coefficients that are statistically significant at $P < 0.05$.

0.1–2.2 meters). The plants aged 3–4 years were located at a distance of 1.24 ± 0.04 meters from older individuals of the same species (95% percentile 0.2–4.0 meters). The kurtosis of the distribution was positive and amounted to 2.75 ± 0.13, indicating the prevalence of modal values with a probability higher than the random alternative. The plants aged 6–8 years exhibited transient values of distances, but a bimodal distribution with maxima corresponding to small and large values of distances. The kurtosis of the distribution was positive and amounted to 0.76 ± 0.31. The distribution was "sharper" than normal due to a significant predominance of smaller distances. The Kolmogorov-Smirnov test for the mixture of two normal distributions of log-transformed distances was $d = 0.081$, $P = 0.15$. 76% of the mixture is the component with parameters 3.3 ± 0.09 meters and 24% of the mixture is the component with parameters 13.7 ± 0.12 meters. The distance for plants aged 1–5 years was significantly different from the distance for plants aged 6–8 years ($F = 114.6$, $P < 0.001$). The significant differences between plants aged 1–5 years in absolute distance values and in the nature of the statistical distribution compared to plants aged 6–8 years suggest that spreading by root shoots is the predominant mechanism for generating the distance of plants of this age group. The relationship between age and average distance to the nearest older individual was close to linear for plants

Table 3. Fitting of point process models to the observed point pattern of Robinia pseudoacacia distribution in the space of an artificial tree plantation

Polygon	Age class	Homogeneous Poisson process		Non-homogeneous Poisson process with a linear trend			Non-homogeneous Poisson process with linear trend and Widom-Rowlinson model				
		λ_1	AIC_1	λ_2	k_2	AIC_2	r	λ_3	k_3	η	AIC_3
A1	Total	0.17	623.75	0.25	–0.0088*	619.57	1.65	0.003	0.0300	–3.26	30.14
	5–14	0.08	378.87	0.07	0.0048	379.98	1.69	0.00	0.0282	2.73	18.05
	15–45	0.05	270.75	0.12	–0.0210*	262.85	1.20	0.06	–0.0304*	2.96	67.43
	50+	0.04	201.78	0.11	–0.0325*	189.54	0.53	0.07	–0.0226	–4.03	139.60
A2	Total	0.15	569.13	0.12	0.0055	569.00	1.66	0.64	0.0169	–3.75	35.83
	5–14	0.08	358.65	0.05	0.0088	357.90	1.69	0.00	0.1427*	5.97	10.22
	15–45	0.04	227.86	0.05	–0.0036	229.61	1.06	0.11	–0.0020	–1.87	128.66
	50+	0.03	174.29	0.02	0.0058	175.84	1.12	0.04	0.0042	–7.16	55.29
A3	Total	0.14	549.94	0.20	–0.0073	548.41	0.36	0.16	–0.0051	0.88	431.70
	5–14	0.06	299.57	0.09	–0.0105	298.56	0.55	0.08	–0.0090	0.14	201.22
	15–45	0.03	181.31	0.04	–0.0045	183.03	0.75	0.04	–0.0042	1.82	110.35
	50+	0.03	167.17	0.03	0.0005	169.17	1.20	0.00	0.0557	–6.20	24.31
A4	Total	0.14	534.20	0.28	–0.0179*	516.99	0.57	0.17	–0.0136*	1.63	323.83
	5–14	0.05	252.76	0.13	–0.0257*	241.88	0.64	0.14	–0.0268	0.40	164.24
	15–45	0.05	264.81	0.14	–0.0282*	250.63	1.69	0.15	–0.1189*	2.18	12.29
	50+	0.03	195.05	0.03	0.0042	196.77	0.74	0.01	0.0274*	–6.57	101.34

λ_1 is the intensity of the homogeneous Poisson process (trees m^{-2}), λ_2 and λ_3 are the free term of the nonhomogeneous Poisson process model, k_2 and k_3 are the linear trend, r is the radius of the disks in the area interaction process, or the irregular parameter of the Widom-Rowlinson model found by maximizing the AIC criterion, η is the interaction parameter, which can be any positive number: If $\eta = 1$, then the model reduces to a Poisson process with intensity λ_3; if $\eta < 1$, then the process is regular, and if $\eta > 1$, then the process is clustered. Two points interact if the distance between them is less than 2r. Asterisk (*) denotes coefficients that are statistically significant at $P < 0.05$.

Table 4. Spatial segregation of plant species and age groups in the area of spontaneous distribution and artificial tree plantation. Dixon's spatial segregation index is positive when the frequency of occurrence of a species in the environment is greater than the probability of a random alternative. The index is negative when the frequency of occurrence is less likely than the random alternative. N indicates the number of statistically significant indices for $P < 0.05$ after 999 simulations.

From	To	Spontaneous spreading		Artificial planting	
		N	S ± st. error	N	S ± st. error
Robinia pseudoacacia 1–2	*Robinia pseudoacacia* 1–2	2	0.44 ± 0.05	–	–
Robinia pseudoacacia 1–2	*Robinia pseudoacacia* 3–4	3	0.48 ± 0.11	–	–
Robinia pseudoacacia 1–2	*Robinia pseudoacacia* 5–14	5	–0.63 ± 0.10	–	–
Robinia pseudoacacia 3–4	*Robinia pseudoacacia* 1–2	4	0.40 ± 0.07	–	–
Robinia pseudoacacia 3–4	*Robinia pseudoacacia* 3–4	2	0.21 ± 0.01	–	–
Robinia pseudoacacia 3–4	*Robinia pseudoacacia* 5–14	2	–0.61 ± 0.21	–	–
Robinia pseudoacacia 5–14	*Robinia pseudoacacia* 1–2	4	–0.51 ± 0.10	–	–
Robinia pseudoacacia 5–14	*Robinia pseudoacacia* 3–4	2	–0.33 ± 0.12	–	–
Robinia pseudoacacia 5–14	*Robinia pseudoacacia* 5–14	4	0.45 ± 0.11	2	0.76 ± 0.01
Robinia pseudoacacia 5–14	*Robinia pseudoacacia* 15–45	–	–	2	–0.20 ± 0.54
Robinia pseudoacacia 15–45	*Robinia pseudoacacia* 15–45	–	–	2	0.70 ± 0.05
Robinia pseudoacacia 50	*Cotinus coggygria*	–	–	2	–0.35 ± 0.01
Fraxinus pennsylvanica	*Fraxinus pennsylvanica*	–	–	2	1.50 ± 0.39
Fraxinus pennsylvanica	*Robinia pseudoacacia* 3–4	3	–0.56 ± 0.13	–	–
Ulmus minor	*Ulmus minor*	2	1.0 ± 0.36	–	–
Cotinus coggygria	*Cotinus coggygria*	–	–	3	0.91 ± 0.30
Prunus spinosa	*Prunus spinosa*	–	–	2	0.67 ± 0.13

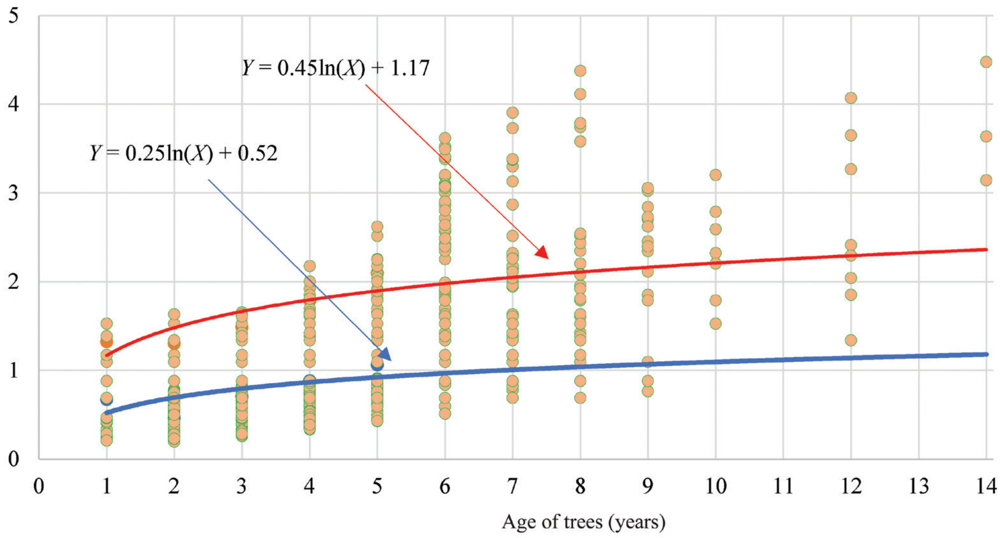

Fig. 2. Dependence of the smallest distances of *R. pseudoacacia* individuals from older individuals of the species within spontaneous distribution or in artificial tree plantation. The abscissa is the age of the trees (in years); the ordinate is the distance of *R. pseudoacacia* individuals from older individuals of this species (in meters) (after ln(x+1) transformation). The blue line shows an approximation of the average distance dependence for trees aged 1–5 years, which was extended to 14 years. The red line shows an approximation of the dependence of the boundary that limits 99% of the distances for trees aged 1–5 years, which is extended to 14 years.

aged 1–5 years and could be described by the equation:

$Y = 0.37 * X$ ($R^2 = 0.95$),

where Y is the average distance to the nearest older individual (in meters); X is the age of the plants, years.

For the upper bound, which was the mean + 3 sigma, i.e., the boundary within which 99% of the observations fell, the dependence was as follows:

$Y = 1.36 * X$ ($R^2 = 0.93$),

where Y is the greatest distance to the nearest older individual, which is not exceeded by observations in 99% of cases (in meters); X is the age of plants (in years).

Thus, the increase in the distance between individuals can be assumed to be a consequence of the growth of root shoots. In this case, the estimate of the rate of spread of the Robinia community is equal to the regression coefficient of the corresponding model. The community spreads on average at a rate of ≈0.4 m year–1 due to the growth of sprouts, and in 99% of cases the spread rate does not exceed ≈1.4 m year^{-1}.

Discussion

The age structure of the *R. pseudoacacia* population in the artificial tree plantation and in spontaneous dispersal zone differs significantly. The spontaneous dispersal has a dominant modal class, and the age distribution is shifted to the left, indicating a moderate rate of community spread in the early stages of development and the rapid occurrence of the terminal phase within 14 years after the first plants appeared. The artificial plantation was formed by the plants of the same age from the beginning of 50 years of the last century. The durability of monodominant artificial stands of *R. pseudoacacia* in Europe, where they can exist for more than 70 years, is explained by the limited pool of native tree species in most invasive areas and the absence of serious natural enemies (Vítková and Kolbek, 2010). In addition, a dense cover of grasses and sedges can slow down forest succession (Terwei et al., 2016). Over time, the plantation, which was made in straight rows, suffered the loss of individual trees, and the emerging glades triggered a mechanism of regenerative succession with the growth of younger *R. pseudoacacia* species, which in some ways was similar to what is now observed in spontaneous dispersal zone. Such excesses of restorative succession had three features. First, it is the area of plots where younger plants grew. Within the artificial plantation, these areas were much smaller than in the area of spontaneous spread. Secondly, it is the duration of active spread of plants. The signs of the terminal phase are observed in the spontaneous spread zone after 14 years of spread, while in the artificial forest plantation zone, almost discrete age classes unite plants with an age range of about 5 years. Thirdly, the community in the area of spontaneous spread is represented by almost one species of *R. pseudoacacia* with few representatives of other invasive species such as *Acer negundo* and *Fraxinus pennsylvanica*. This is fully consistent with the findings that among the sites spontaneously colonized by *R. pseudoacacia*, pure stands are typical, which usually make up two-thirds of the total area of the territories where this species has spread (Ivajnsic et al., 2012). Gaps within the artificial plantation are being restored by new generations of *R. pseudoacacia*, as well as by a wide range of autochthonous shrubs and trees such as *Acer tataricum*, *Crataegus monogyna*, *Euonymus verrucosa*, *Prunus spinosa*, *Pyrus communis*, *Quercus robur*, and others. *Robinia* is a relatively weak competitor and occurs in mixed stands of fast-growing early successional species, in both native and alien, namely among the trees such as *Acer negundo* and *Ailanthus altissima*, as well as among the shrubs such as *Prunus spinosa* (Kowarik et al., 2013). There is evidence that seedlings of slow-growing native trees, such as oaks, lose in competition with *Robinia* (Vítková et al., 2017).

The recorded spatial distribution and spatial associations of species or their age groups can form the basis for hypotheses about the underlying processes of spatial distribution. A positive spatial association indicates that species are dependent on each other and that they respond to the environment in a similar way. A negative spatial association indicates that species respond differently to the environment or that one species excludes another (Ben-Said, 2021). Spatial associations may also result from factors such as differential resource use, dispersal and germination mechanisms, or reproductive strategies (Ågren et al., 1984). The spatial distribution within a species can vary from clustered to regular, depending on dispersal and ability to re-sprout (Call and Nilsen, 2003). The differences between artificial tree plantation and spontaneous spreading zone are also evident in the analysis of point process patterns. In both cases, the spatial process cannot be described by a random alternative modeled only by a Poisson process. The analysis of the spatial distribution of *R. pseudoacacia* within the native range showed the presence of clusters of plants due to the large number of root shoots growing from individuals (Call and Nilsen, 2003). First-order factors (exogenous effects) and second-order factors (endogenous interactions) are needed to explain the point process. The first-order factor, or linear trend, may be the result of seed dispersal processes that, within a certain distance, depend linearly on the distance from the parent tree. The distance to the nearest artificial tree plantation is known to be a factor in the spread of *R. pseudoacacia* in abandoned fields and pastures (Ivajnsic et al., 2012). Our results indicate that a linear trend is a characteristic feature of the spatial point process within spontaneous dispersal. This is in line with the findings that, regardless of the characteristics of the area where the spread occurs, the proportion of settlement and the intensity of *R. pseudoacacia* spread decreases by the distance to the original plantation (Carl et al., 2019). A linear trend can also be observed in the artificial tree plantation, but the nature of this trend is quite different. A linear trend is the result of the loss of some of the old trees and the contrast in conditions that prevail in the trend. This explains the fact that the most frequent linear trend in artificial forest plantations was observed for age classes younger than 50 years.

The second-order factors also have a different nature in the artificial plantation and in the spontaneous dispersal zone. The second-order factors in spontaneous dispersal zone lead to aggregated distribution of plants, which can be explained by the result of plants spreading by means of root shoots, the length of which is limited, so the parent plant and its offspring are aggregated in space. The aggregation is also observed in the artificial tree plantations for younger plant age groups, which can also be explained by vegetative spread. *R. pseudoacacia* is known to produce numerous root shoots even on trees over 70 years old (Vítková and Kolbek, 2010). The spatial distribution of the oldest age group of trees that were planted for the first time was regular, which is fully consistent with the technology of creating artificial tree plantation.

The clonal ability of *R. pseudoacacia* to spread is significant, with the rate of spread of spontaneous growth from the original artificial plantations on different soil types and in different types of ecosystems ranging from 0.75–1 m according to various estimates (Kowarik, 1996) up to 2.0–2.2 m per year (Crosti et al., 2016). These results are in full agreement with our estimates of the rate of spread to be ≈ 0.4 m year^{-1} through sprout growth and in 99% of cases the rate of spread does not exceed ≈ 1.4 m year^{-1}. In the process of spreading, local clonal colonies are formed, the area of which can reach from several hundred (Krízsik and Körmöczi, 2000) to 10,000 square meters (Chang et al., 1998). Soil and climatic conditions determine the spread rate via vegetative root suckers. Various authors have reported a spread of 50 (Crosti et al., 2016) to 100 metres (Kowarik, 2010) within 20 years. At the same time, despite significant clonal integration between the mother plant and offspring ramets (Zhang et al., 2006), translocation processes between them stop after a few years (Jung et al., 2009). The presence of long-term clonal integration in alien clonal species is considered as one of the factors of successful invasions into autochthonous plant communities, especially with a high degree of disturbance and eutrophication of habitats (Wang et al., 2022). The speed and intensity of colonization of adjacent habitats by the *R. pseudoacacia* shoots considerably influences the vegetation composition, the existence or lack of disturbances of soil and vegetation cover, and the peculiarities of agricultural activities (Tutova et al., 2023). The vegetative activity of *R. pseudoacacia* with the formation of a larger number of ramets increases under high light levels in open areas and, on the contrary, decreases under shade (Carl et al., 2019). This minimizes the potential danger of colonization of natural broadleaf forests with undisturbed canopy (Vítková et al., 2017), but promotes the active settlement of acacia in the adjacent to the plantations lighted areas of meadows, steppes, roadsides, etc. (Zhukov et al., 2023).

Knowledge of the spatial distribution of *R. pseudoacacia* plants and the age of plants allows us to make assumptions about the reconstruction of the dynamics of spontaneous spread of this plant on fallow land. Retrospective satellite imagery indicates that study area has been out of agricultural use and has not been plowed since about 2005. The oldest *R. pseudoacacia* plants found in the area of spontaneous spread were 14 years old in 2022, meaning that the growth of these plants began in 2008. Thus, there was a period of three years before the spread began and the area was no longer used for agricultural production. It can be assumed that during this time, phytomass accumulated on the field that could have been burned, as farmers often use stubble burning as a measure against diseases and pests (Yakovenko et al., 2023). Fire from the fields easily spreads to the surrounding areas. Such a fire could trigger a pyrogenic succession to which *R. pseudoacacia* is adapted under natural conditions (Gongalsky, 2014). *R. pseudoacacia* was propagated by seeds in the initial stages of spontaneous spread. This assumption is confirmed by our data, since the oldest plants were located at a considerable distance from the source of spread, which cannot be explained by the spread by root shoots. It is reported that at short distances, except for areas with shady, humid or constantly disturbed conditions, *R. pseudoacacia* spreads locally up to 1 m per year due to horizontal root elongation and formation of ramets that form a connected root system (Kowarik, 1996).

The distribution of distances to the nearest older plants, which could hypothetically be the parent, is well described by a normal law in plants aged 9–14 years, indicating that the causes of variability in this trait are the same. All plants of this age group were usually located at a distance greater than would be expected from root sprouting. Thus, during the first period of Robinia's spread, it was mainly due to seed reproduction. This process was not constant, as there are no plants aged 11 and 13 years among our collections. The plants aged 8 years are close either to an artificial tree plantation, which could be a source of *R. pseudoacacia* spread, or to the older plants that started their existence from seeds. The stage of 6–8 years is characterized by a combination of two strategies of spreading: by seeds and by root shoots. This duality is manifested in the bimodal distribution of distances, which is characteristic of this stage of spontaneous community existence. *R. pseudoacacia* can spread by means of seeds and root shoots. There is evidence that the short-distance spread of the species by means of root shoots is superior to the seed spread (Huntley, 1990). Our data indicate that plants 6 years old are already located within the entire area that is now covered by spontaneous community. Thus, the combination of seed and root spread allowed *R. pseudoacacia* to move 86–90 meters in 8 years. These results are in good agreement with the information that the spread of root shoots usually begins when the plants are 4 years old and grow rapidly in the open sunny areas (Grese, 1991). Subsequently, the geographical spread of *R. pseudoacacia* practically ceased, and the development of the community was aimed at increasing its density. The plants aged 1–5 years were placed at a distance from the probable parental individuals, which can be explained by the spread by root shoots. The density of plants aged 2 years should also be noted to be quite high, while the density of plants aged 1 year was much lower, which may indicate the terminal stage of the dynamics of *R. pseudoacacia* spreading, which is marked by the termination of both seed and vegetative spread. The mechanical damage to roots or trunks leads to an increase in the density of trunks and rejuvenation of *R. pseudoacacia* stands, which leads to the spread of concentrated clonal colonies occupying areas of several hundred square meters (Krízsik and Körmöczi, 2000). Our results suggest that the view that spontaneous spread of *R. pseudoacacia* from artificial tree plantations occurs primarily through root shoots (Carl et al., 2019) does not fully reflect the actual dynamics of the species' spread. The observed distance of trees from probable parental individuals in the first years of distribution cannot be explained exclusively by the vegetative mechanism of distribution. The observed spatial patterns indicate a gradual substitution of the predominance of the seed mechanism of *R. pseudoacacia* spread by the vegetative one during the development of the spontaneous community.

Conclusion

The reconstruction of the dynamics of plant community formation in the area of spontaneous *R. pseudoacacia* spread along with the analysis of point patterns give consistent results which indicate that seed and vegetative reproduction play an important role in spread of the *R. pseudoacacia* in the areas where agricultural production has been discontinued. Fire, which is provoked by farmers as a result of regular stubble burning, is most likely to be a trigger for the spread. In the early stages, the seed reproduction is the most probable process of *R. pseudoacacia* spread. The source of seed generation is an artificial tree plantation. Young trees appear randomly within the space where seed dispersal is possible. The stage of predominance of seed spread lasts approximately 5–6 years. The seed dispersal mechanism creates a spatial pattern that is explained by a linear trend. The next stage is a combination of seed and vegetative mechanisms of spread, which also lasts about 4–5 years. The spread through root shoots creates a pattern explained by the Widom-Rowlinson model. This stage results in a community with dense crown closure, which inhibits the seed mechanism of spread. At the last stage, the spread occurs mainly through the vegetative mechanism, and the rate of spread of the community is greatly slowed down. This stage lasts 4–5 years. Similar processes of regeneration are observed in artificial tree plantations as well, but they have a smaller area, duration and occur with the participation of native species, which in the future can replace the adventive species in the structure of the community.

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References

Ågren, G.I., Fagerström, T., Agren, G.I., Fagerstrom, T., 1984. Limiting dissimilarity in plants: Randomness prevents exclusion of species with similar competitive abilities. *Oikos*, 43 (3): 369. https://doi.org/10.2307/3544155

Baddeley, A., Turner, R., Mateu, J., Bevan, A., 2013. Hybrids of Gibbs point process models and their implementation. *Journal of Statistical Software*, 55 (11): 1–43. https://doi.org/10.18637/jss.v055.i11

Ben-Said, M., 2021. Spatial point-pattern analysis as a powerful tool in identifying pattern-process relationships in plant ecology: an updated review. *Ecological Processes*, 10 (1): 56. https://doi.org/10.1186/s13717-021-00314-4

Call, L.J., Nilsen, E.T., 2003. Analysis of spatial patterns and spatial association between the invasive tree-of-heaven (Ailanthus altissima) and the native Black Locust (Robinia pseudoacacia). *The American Midland Naturalist*, 150 (1): 1–14. https://doi.org/10.1674/0003-0031(2003)150[0001:AOSPAS]2.0.CO;2

Carl, C., Biber, P., Landgraf, D., Buras, A., Pretzsch, H., 2017. Allometric models to predict aboveground woody biomass of Black Locust (Robinia pseudoacacia L.) in short rotation coppice in previous mining and agri cultural areas in Germany. *Forests*, 8 (9): 328. https://doi.org/10.3390/f8090328

Carl, C., Lehmann, J., Landgraf, D., Pretzsch, H., 2019. Robinia pseudoacacia L. in short rotation coppice: seed and stump shoot reproduction as well as UAS-based spreading analysis. *Forests*, 10 (3): 235. https://doi.org/10.3390/f10030235

Chang, C.-S., Bongarten, B., Hamrick, J., 1998. Genetic structure of natural populations of black locust (Robinia pseudoacacia L.) at Coweeta, North Carolina. *Journal of Plant Research*, 111 (1): 17–24. https://doi org/10.1007/BF02507146

Crosti, R., Agrillo, E., Ciccarese, L., Guarino, R., Paris, P., Testi, A., 2016. Assessing escapes from short rotation plantations of the invasive tree species Robinia pseudoacacia L. in Mediterranean ecosystems: a study in central Italy. *IForest - Biogeosciences and Forestry*, 9 (5): 822–828. https://doi.org/10.3832/ifor1526-009

De la Cruz, M., 2008. Metodos para analizar datos puntuales [Techniques for analysis of point data]. In Maestre, F.T., Escudero, A., Bonet, A. (eds). *Introduccion al analisis espacial de datos en ecologia y ciencias ambientales: metodos y aplicaciones, Asociacion Espanola de Ecologia Terrestre.* Madrid: Universidad Rey Juan Carlos y Caja de Ahorros del Mediterraneo, p. 76–127.

Dixon, P.M., 2002. Nearest-neighbor contingency table analysis of spatial segregation for several species. *Écoscience*, 9 (2): 142–151. https://doi.org/10.1080/11956860.2002.11682700

ESRI, 2011. *ArcGIS desktop: release 10*. Redlands, CA, USA: Environmental Systems Research Institute.

Gongalsky, K.B., 2014. *Lesnye pozhary i pochvennaya fauna* [Wildfires and soil fauna]. Moskva: KMK. 169 p.

Grese, R., 1991. The landscape architect and problem exotic plants. In Burley, J.B. (eds), *Proceedings of the American Society of Landscape Architects' Open Committee on Reclamation: Reclamation Diversity, San Diego, CA, USA, 29 October 1991*. Washington, DC, USA: American Society of Landscape Architects, p. 7–15.

Holoborodko, K.K., Sytnyk, S.A., Lovynska, V.M., Ivanko, I.A., Loza, I.M., Brygadyrenko, V.V., 2022. Impact of invasive species Parectopa robiniella (Gracillariidae) on fluorescence parameters of Robinia pseudoacacia in the conditions of the steppe zone of Ukraine. *Regulatory Mechanisms in Biosystems*, 13 (3): 324–330. https://doi.org/10.15421/022242

Huntley, J.C., 1990. Robinia pseudacacia L. Black locust. In Burns, R.M., Honkala, B.H. (eds). *Silvics of North America. Vol. 2. Hardwoods*. Agriculture Handbook (United States. Department of Agriculture), no. 654. Washington, DC: United States Government Printing Office, p. 755–761.

Ivajnsic, D., Cousins, S., Kaligarič, M., 2012. Colonization by Robinia pseudoacacia of various soils and habitat types outside woodlands in a traditional Central-Europen agricultural landscape. *Polish Journal of Ecology*, 60: 301–309.

Jeník, J., 1994. Clonal growth in woody plants: a review. *Folia Geobotanica et Phytotaxonomica*, 29 (2): 291–306. https://doi.org/10.1007/BF02803802

Jírová, A., Klaudisová, A., Prach, K., 2012. Spontaneous restoration of target vegetation in old-fields in a central European landscape: a repeated analysis after three decades. *Applied Vegetation Science*, 15 (2): 245–252. https://doi.org/10.1111/j.1654-109X.2011.01165.x

Jung, S.-C., Matsushita, N., Wu, B.-Y., Kondo, N., Shiraishi, A., Hogetsu, T., 2009. Reproduction of a Robinia pseudoacacia population in a coastal Pinus thunbergii windbreak along the Kujukurihama Coast, Japan. *Journal of Forest Research*, 14 (2): 101–110. https://doi.org/10.1007/s10310-008-0109-1

Kowarik, I., 1996. Funktionen klonalen Wachstums von Bäumen bei der Brachflächen-Sukzession unter besonderer Beachtung von Robinia pseudoacacia [Functions of clonal growth in trees during wasteland succession with special reference to Robinia pseudoacacia]. *Verhandlungen der Gesellschaft für Okologie*, 26: 173–181.

Kowarik, I., 2010. *Biologische Invasionen: Neophyten und Neozoen in Mitteleuropa* [Biological invasions: new plant and animal species in Central Europe]. Stuttgart, Germany: Ulmer.

Kowarik, I., Lippe, M., Cierjacks, A., 2013. Prevalence of alien versus native species of woody plants in Berlin differs between habitats and at different scales. *Preslia*, 85: 113–132.

Krízsik, V., Körmöczi, L., 2000. Spatial spreading of Robinia pseudo-acacia and Populus alba clones in sandy habitats. *Tiscia*, 32: 3–8.

Kunakh, O.M., Ivanko, I.A., Holoborodko, K.K., Volkova, A.M., Zhukov, O.V., 2023. Age estimation of black locust (Robinia pseudoacacia) based on morphometric traits. *Biosystems Diversity*, 31 (2): 222–228. https://doi.org/10.15421/012324

Lovynska, V., Holoborodko, K., Ivanko, I., Sytnyk, S., Zhukov, O., Loza, I., Wiche, O., Heilmeier, H., 2023. Heavy metal accumulation by Acer platanoides and Robinia pseudoacacia in an industrial city (Northern Steppe of Ukraine). *Biosystems Diversity*, 31 (2): 246–253. https://doi.org/10.15421/012327

Maringer, J., Wohlgemuth, T., Neff, C., Pezzatti, G.B., Conedera, M., 2012. Post-fire spread of alien plant species in a mixed broad-leaved forest of the Insubric region. *Flora - Morphology, Distribution, Functional Ecology of Plants*, 207 (1): 19–29. https://doi.org/10.1016/j.flora.2011.07.016

Nadal-Sala, D., Hartig, F., Gracia, C.A., Sabaté, S., 2019. Global warming likely to enhance black locust (Robinia pseudoacacia L.) growth in a Mediterranean riparian forest. *Forest Ecology and Management*, 449: 117448. https://doi.org/10.1016/j.foreco.2019.117448

Nicolescu, V.-N., Rédei, K., Mason, W.L., Vor, T., Pöetzelsberger, E., Bastien, J.-C., … Pástor, M., 2020. Ecology, growth and management of black locust (Robinia pseudoacacia L.), a non-native species integrated into European forests. *Journal of Forestry Research*, 31

(4): 1081–1101. https://doi.org/10.1007/s11676-020-01116-8

Puchałka, R., Dyderski, M.K., Vítková, M., Sádlo, J., Klisz, M., Netsvetov, M., … Jagodziński, A. M., 2021. Black locust (Robinia pseudoacacia L.) range contraction and expansion in Europe under changing climate. *Global Change Biology*, 27 (8): 1587–1600. https://doi.org/10.1111/gcb.15486

Pyšek, P., Chytrý, M., Pergl, J., Sádlo, J., Wild, J., 2012. Plant invasions in the Czech Republic: current state, introduction dynamics, invasive species and invaded habitats. *Preslia*, 84: 575–629.

R Core Team, 2020. R: a language and environment for statistical computing. Vienna, Austria: *R Foundation for Statistical Computing*. [cit. 2023-12-12]. https://www.R-project.prg

Radtke, A., Ambrass, S., Zerbe, S., Tonon, G., Fontana, V., Ammer, C., 2013. Traditional coppice forest management drives the invasion of Ailanthus altissima and Robinia pseudoacacia into deciduous forests. *Forest Ecology and Management*, 291: 308–317. https://doi.org/10.1016/j.foreco.2012.11.022

Sádlo, J., Vítková, M., Pergl, J., Pyšek, P., 2017. Towards site-specific management of invasive alien trees based on the assessment of their impacts: the case of Robinia pseudoacacia. *NeoBiota*, 35: 1–34. https://doi.org/10.3897/neobiota.35.11909

Samoilych, K.O., Mokritskaia, T.P., 2016. Change in the parameters the microstructure of loess soil during filtration. *Journal of Geology, Geography and Geoecology*, 24 (2): 106–113. https://doi.org/10.15421/111638

Środek, D., Rahmonov, O., 2021. The properties of Black Locust Robinia pseudoacacia L. to selectively accumulate chemical elements from soils of ecologically transformed areas. *Forests*, 13 (1): 7. https://doi.org/10.3390/f13010007

StatSoft Inc., 2014. *STATISTICA Data Analysis Software System, Version* 12.0, 1984-2014. Palo Alto, CA, USA: TIBCO Software Inc. [cit. 2023-12-01] http://Statistica.io

Terwei, A., Zerbe, S., Mölder, I., Annighöfer, P., Kawaletz, H., Ammer, C., 2016. Response of floodplain understorey species to environmental gradients and tree invasion: a functional trait perspective. *Biological Invasions*, 18 (10): 2951–2973. https://doi.org/10.1007/s10530-016-1188-0

Tutova, G.F., Kunakh, O.M., Yakovenko, V.M., Zhukov, O.V., 2023. The importance of relief for explaining the diversity of the floodplain and terrace soil cover in the Dnipro River valley: the case of the protected area within the Dnipro-Orylskiy Nature Reserve. *Biosystems Diversity*, 31 (2): 177–190. https://doi.org/10.15421/012319

Tutova, G.F., Zhukov, O.V, Kunakh, O.M., Zhukova, Y.O., 2022. Response of earthworms to changes in the aggregate structure of floodplain soils. *IOP Conference Series:Earth and Environmental Science*, 1049 (1): 012062. https://doi.org/10.1088/1755-1315/1049/1/012062

van Groenendael, J.M., Klimes, L., Klimesova, J., 1996. Comparative ecology of clonal plants. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 351 (1345): 1331–1339. https://doi.org/10.1098/rstb.1996.0116

Vítková, M., Kolbek, J., 2010. Vegetation classification and synecology of Bohemian Robinia pseudacacia stands in a Central European context. *Phytocoenologia*, 40 (2–3): 205–241. https://doi.org/10.1127/0340-269X/2010/0040-0425

Vítková, M., Müllerová, J., Sádlo, J., Pergl, J., Pyšek, P., 2017. Black locust (Robinia pseudoacacia) beloved and despised: a story of an invasive tree in Central Europe. *Forest Ecology and Management*, 384: 287–302. https://doi.org/10.1016/j.foreco.2016.10.057

Wang, Y., Liu, Y., Chen, D., Du, D., Müller-Schärer, H., Yu, F., 2024. Clonal functional traits favor the invasive success of alien plants into native communities. *Ecological Applications*. https://doi.org/10.1002/eap.2756

Yakovenko, V., Kunakh, O., Tutova, H., Zhukov, O., 2023. Diversity of soils in the Dnipro River valley (based on the example of the Dnipro-Orilsky Nature Reserve). *Folia Oecologica*, 50 (2): 119–133. https://doi.org/10.2478/foecol-2023-0011

Yakovenko, V., Zhukov, O., 2021. Zoogenic structure aggregation in steppe and forest soils. In Dmytruk, Y., Dent, D. (eds). *Soils under stress*. Cham: Springer International Publishing, p. 111–127. https://doi.org/10.1007/978-3-030-68394-8_12

Zhang, X.-Q., Liu, J., Welham, C.V.J., Liu, C.-C., Li, D.-N., Chen, L., Wang, R.-Q., 2006. The effects of clonal integration on morphological plasticity and placement of daughter ramets in black locust (Robinia pseudoacacia). *Flora - Morphology, Distribution, Functional Ecology of Plants*, 201 (7): 547–554. https://doi.org/10.1016/j.flora.2005.12.002

Zhukov, O., Kunakh, O., Yorkina, N., Tutova, A., 2023. Response of soil macrofauna to urban park reconstruction. *Soil Ecology Letters*, 5 (2): 220156. https://doi.org/10.1007/s42832-022-0156-0

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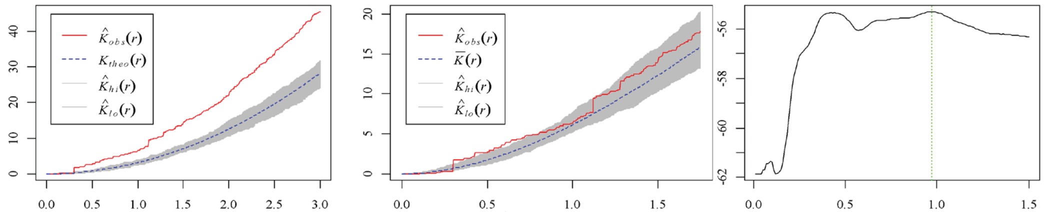
Supplementary material



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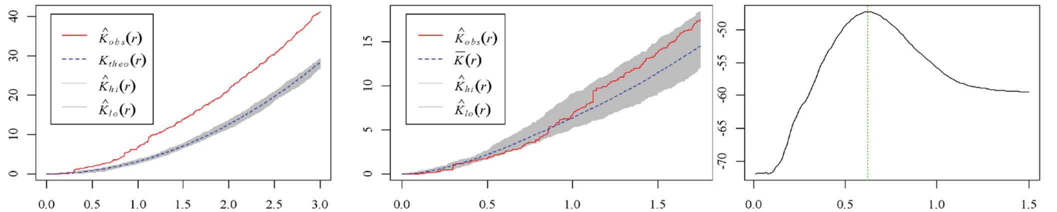

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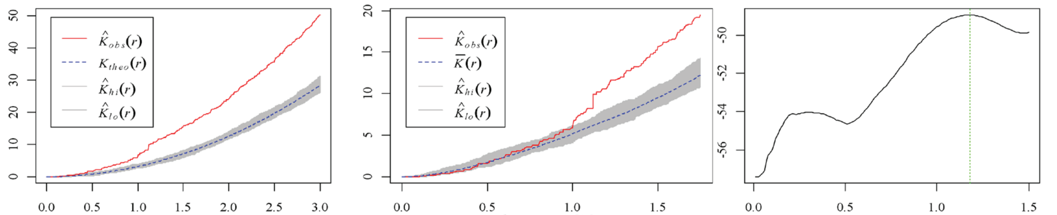

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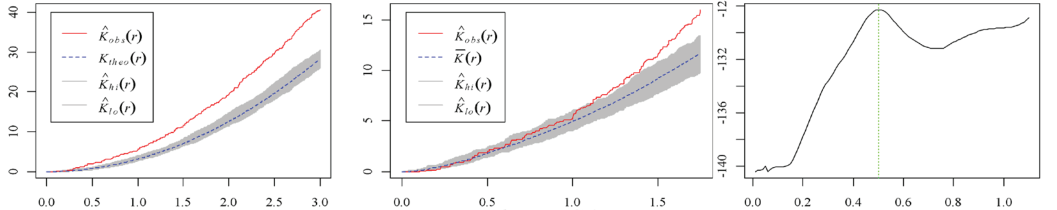

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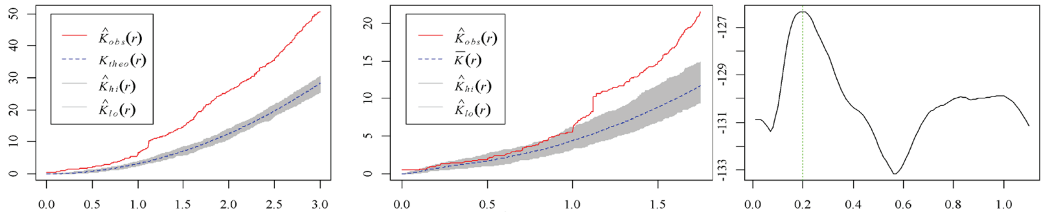

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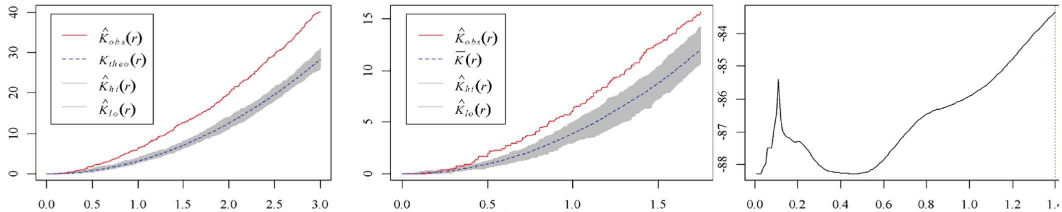

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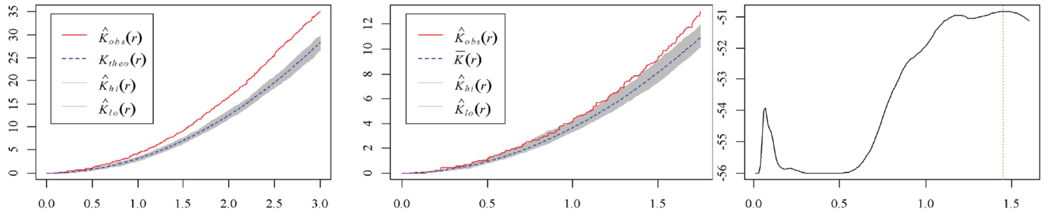
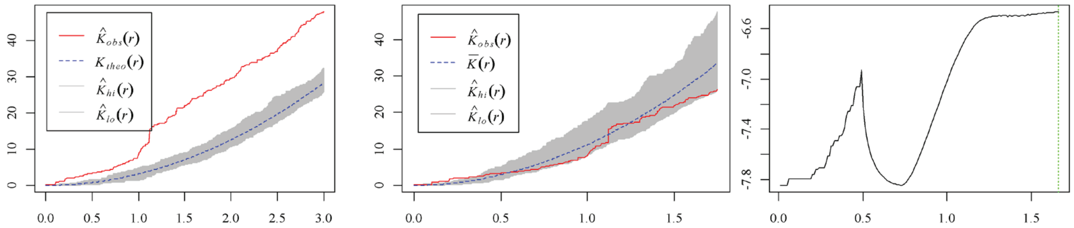


Polygon S7

a b c

Fig. S1. Dependence of the K-function on the interaction radius for a homogeneous Poisson process (a) and a heterogeneous Poisson process with linear trend (b) and the Widom-Rowlinson model of permeable spheres and the search for irregular parameter of the Widom-Rowlinson model by maximizing the AIC criterion (c) for a zone of spontaneous spread of a tree plantation.



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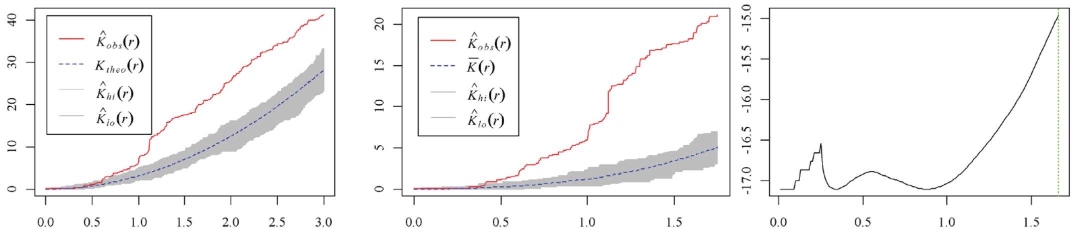

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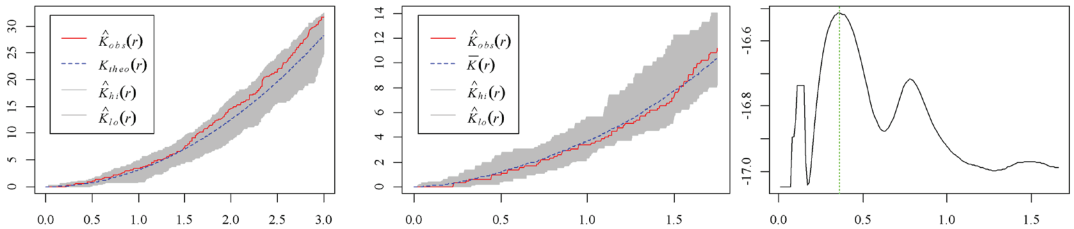

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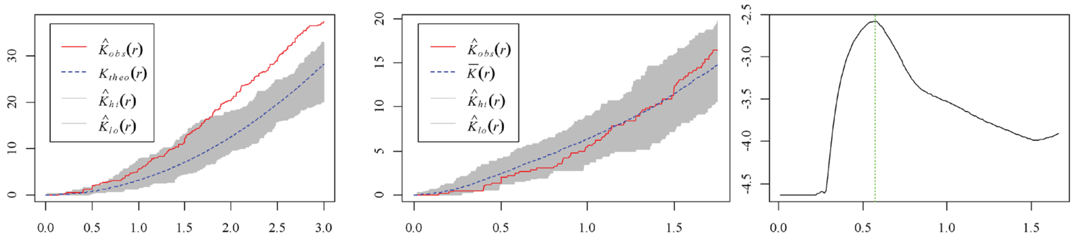
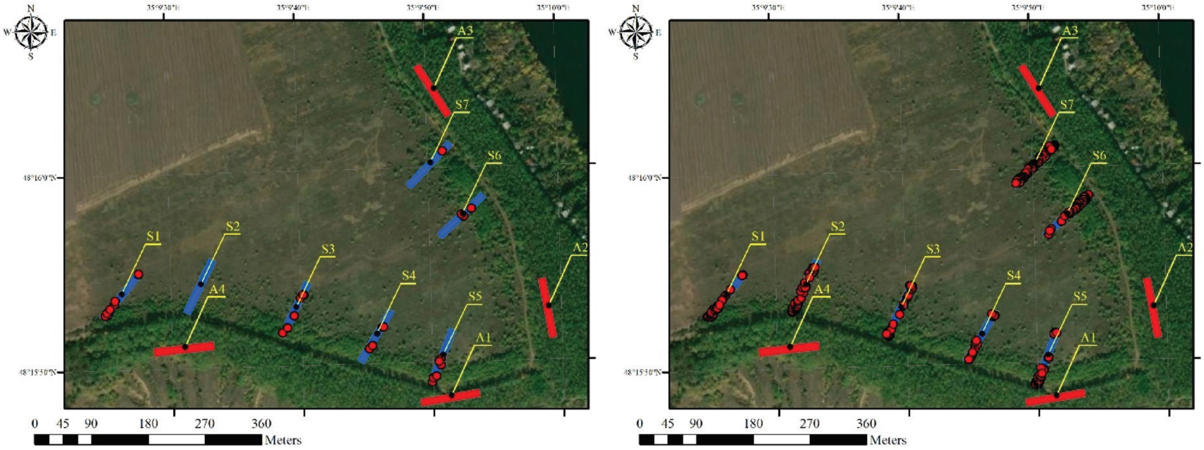


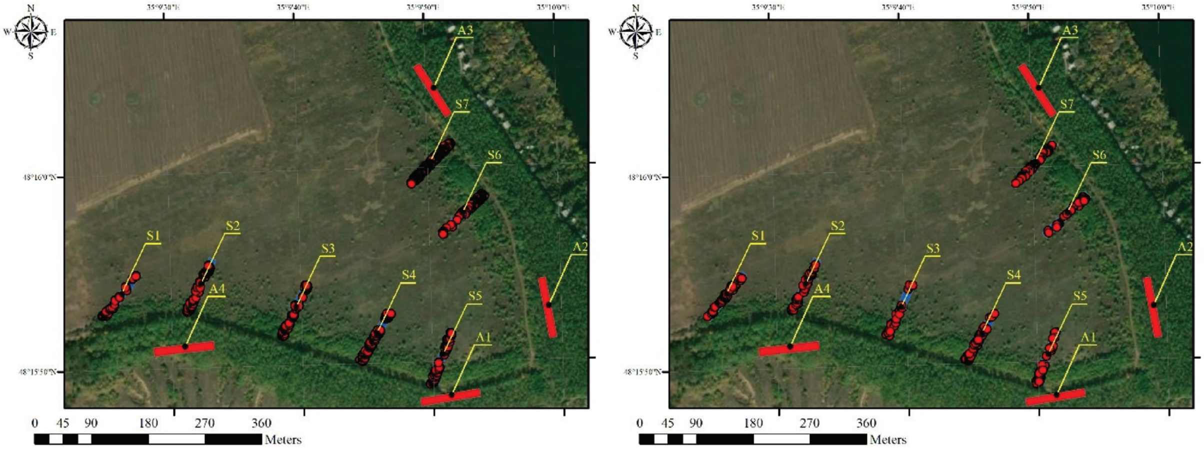
Polygon A4

a b c

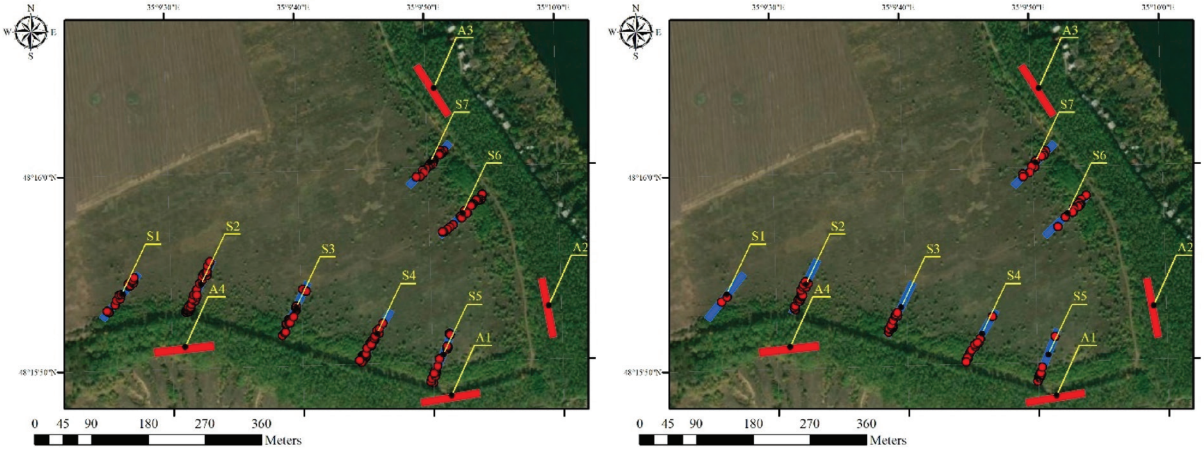
Fig. S2. Dependence of the K-function on the interaction radius for a homogeneous Poisson process (a) and a non-homogeneous Poisson process with linear trend (b) and the Widom-Rowlinson model of permeable spheres and the search for irregular parameter of the Widom-Rowlinson model by maximizing the AIC criterion (c) for artificial tree plantation.



1 year 2 years

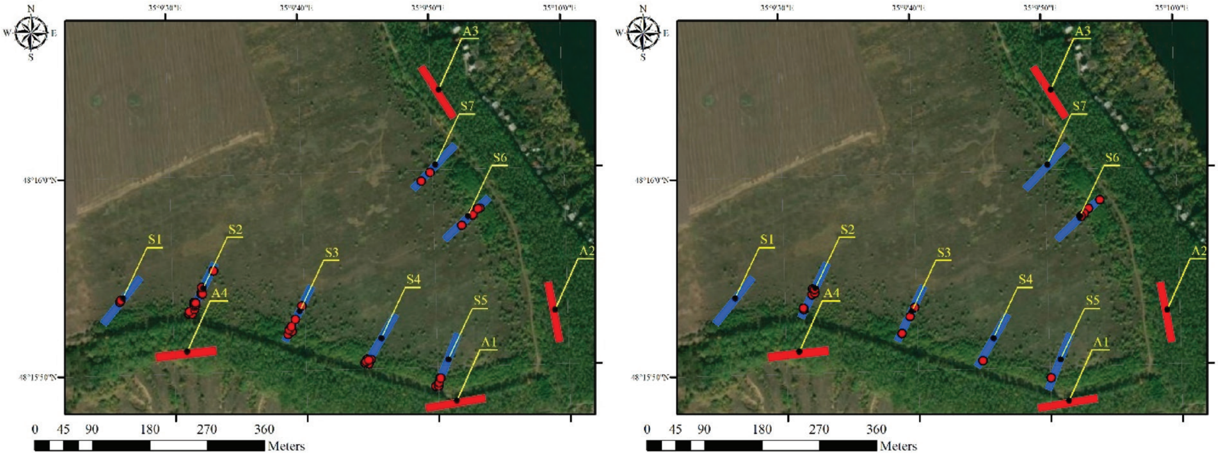


3–4 years 5 years



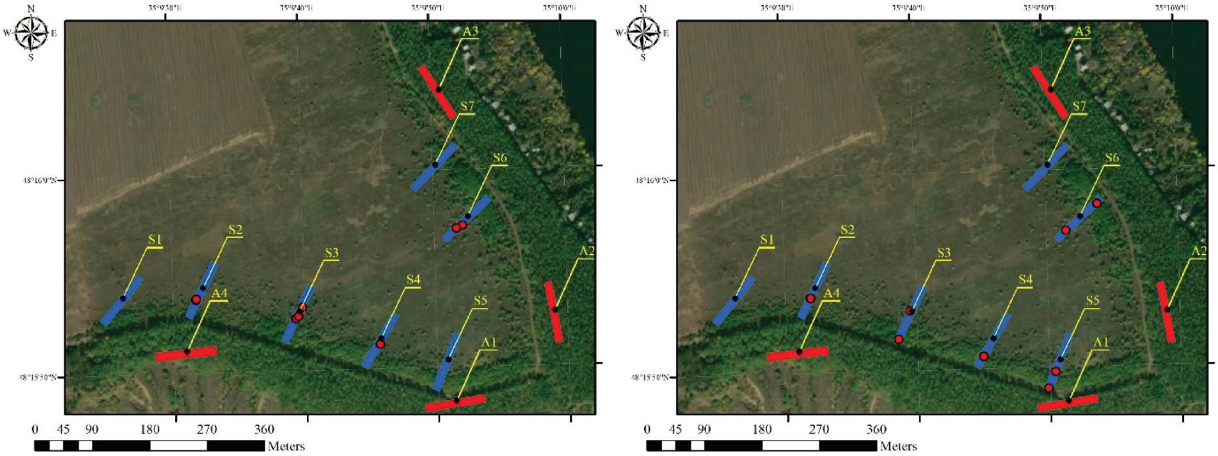
6 years 7 years

Fig. S3. Spatial distribution of *R. pseudoacacia* of different ages within spontaneous dispersal zone.



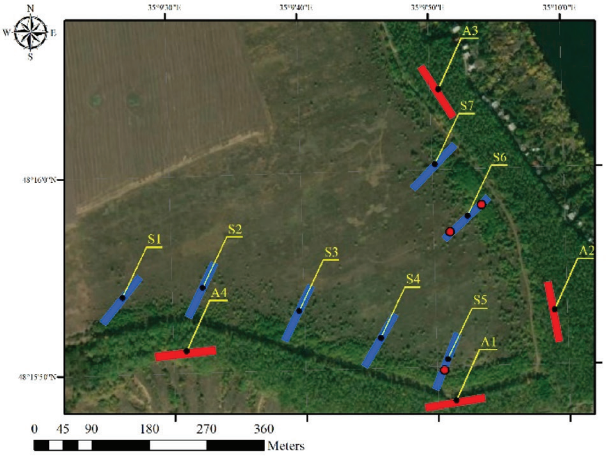
8 years

9 years



10 years

12 years



14 years

Fig. S4. Spatial distribution of *R. pseudoacacia* of different ages within spontaneous dispersal zone.

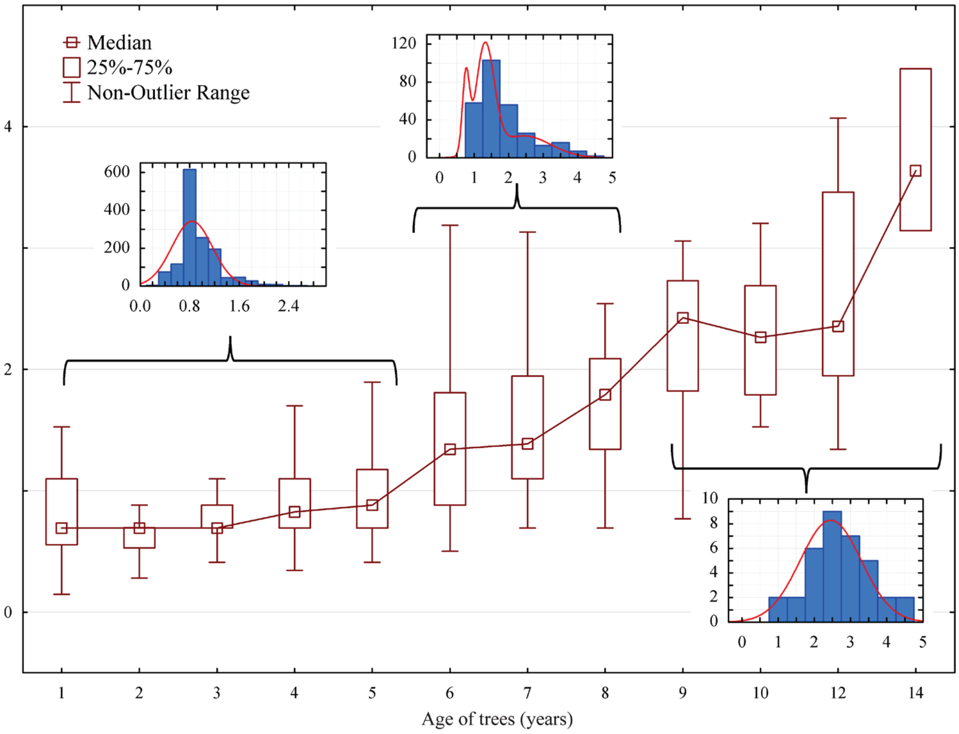


Fig. S5. Box-and-whisker plots and histograms of the smallest distances of *R. pseudoacacia* individuals from older individuals within spontaneous distribution and artificial tree plantation.