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The pattern of seed banks during secondary succession on poor soils

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Abstract

Studies on the soil seed banks of fallow lands of different ages were carried out on poor soil abandoned fields and in a fresh coniferous forest in north-eastern Poland. The size and diversity of seed banks was studied with the seedling emergence method. Species abundance (***i***), density (***ii***), number of species from different biological groups (***iii***) and distribution and mean *LI* value (***iv***) were analysed as the function of fallow land age. It was found that: (***i***) species diversity, number of species and ln of density are linear declining function of the fallow land age; (***ii***) for approx. 25 years the share of diaspores of identified species groups has been relatively similar. Seed banks of 40-50-year-old fallow lands are dominated by *Calluna vulgaris*, while the seed bank of the old fresh coniferous forest is dominated by dicotyledonous perennials and grasses; (***iii***) within the first 50 years of succession the persistence of seed banks measured by the Longevity Index increases gradually.

Keywords: *Calluna vulgaris*, fresh coniferous forest, initial stage, Longevity Index, psammophilous species, secondary succession, persistence

Introduction

In the second half of the 20th century new technologies introduced in Europe, and withdrawal from conventional techniques of plant and animal production caused a marked decrease in agriculturally used area. Secondary succession was initiated on gradually abandoned fields and pastures, unmown meadows and forests after modified use (theory and prediction – [1], abandoned cattle grazing – [2-6], post-fire succession on abandoned fields [7]). During last two decades many studies were published on the correlation between seed banks and secondary succession in various study sites, e.g. on abandoned fields [8], pastures [9], wet meadows and marshlands [10-12], dry and wet grassland [13], heather moorland [14], forest plantations [15], and forest [16,17].

The changes observed in species composition and the size of seed banks during succession indicated that their long-term dynamics is not defined by one pattern. According to Bossuyt and Hermy [18] the species composition of the seed bank in the entire succession series is relatively constant. Species coming mainly from earlier succession phases are present in a seed bank all the time, and they form persistent seed banks. Their diaspores remain in the seed bank for a long time after the plants' disappearance from the ground layer, but the soil diaspores' reserve is not replenished by seed fall. The different pattern describes a situation when over time the density of diasporas or number of species decrease in the consecutive stages. The rate of this process depends on the type of initial community (e.g. succession on grasslands – [19], succession on heather moorlands – [20]).

However, the increasing pattern of changes in the seed bank during succession has been observed in other studies. Species abundance and diaspore density in seed banks increase over time, while their longevity decreases [11,21,22]. The size and species composition of the seed bank in such a case reflect succession transformations in vegetation. Milberg [23] and Falińska [10] described a fluctuating seed bank pattern. Falińska [10] observed the highest species abundance and seed bank density in the transient stage of successional changes, when seeds of species from the previous phases were still present in the soil, but forest species had already appeared. It is worth mentioning that her observation were conducted over 20 years on the same permanent plots.

In 1980 [8] studied species diversity and seed bank density for four fallow lands located on the margin of Białowieża Forest, on poor soils abandoned for 6 to 26 years. Our study continues to some extent work by [8].

In this study we revisited the oldest fallow land studied by Symonides after 13 and 24 years. Faliński [24] concerned that the final stage of successional course in that place would be fresh coniferous forest *Peucedano-Pinetum*. We wanted to determine if soil seed bank of our oldest patches are similar to late successional, stable fresh coniferous forest. Therefore, for soil seed banks comparison we selected the best preserved

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patch of *Peucedano-Pinetum* in Białowieża forest.

The study objective was: (***i***) find out how the persistence of soil seed bank composition and longevity of diasporas in a soil seed bank changes within the entire succession series, taking into account [18] concerns; (***ii***) to establish seed bank pattern for different succession phases.

Material and methods

Study area

All study sites were located near the village of Jelonka (52°35'40"N, 23°22'E) on the south-west margin of Białowieża Primeval Forest. After WWII farming in this area was gradually discontinued on fields located in poor coniferous forest habitats, which has led to the formation of a spatial complex composed of fallow land abandoned at different periods of time. In 1972 Prof. J. B. Faliński began a long-term study and established permanent study plots. In this work, his unpublished data concerning species cover in vegetation were incorporated to our analysis.

In our analyses we used the published data of Symonides [8] concerning the species diversity and density of soil seed banks 6, 10, 16 and 26 years-old abandoned fields. Faliński [24] defined the community which grew on 26 years old fallow land as a brushwood community of *Juniperus communis – Populus tremula – Pinus sylvestris*.

The selected study site (*P-P*), with an old pine woodstand, single spruces and birch, is the best preserved patch (52°39'96"N, 23°43'01"E) of fresh coniferous forest in the Polish part of Białowieża Primeval Forest. Over 70% of its area is covered by ground layer, 90% by bryophytes, and lichens are encountered in the patch sporadically.

Field sampling

Samples for the analyses of the soil seed bank of 39- and 50-years old fallow land were collected in the early spring 1993 and 2004. It worth underlining that it was the same patch which had been studied by Symonides [8]. Soil samples (volume 100 cm^3) were collected with a 5 cm high, 20 cm^2 diameter metal cylinder. Samples were collected at both times from the same 20 plots, each of 25 m^2 surface. From each plot 50 samples were collected (from points within 1 m distance of each other). Samples from the study site *P-P* were collected (after removal of the bryophyte layer) from the upper soil layer (0-5 cm) using the same procedure. The same schedule was applied for the collection of samples from the deeper layer (5-10 cm).

Greenhouse procedure

The species composition and density of seed in the seed bank were determined using the seedling emergence method [25,26]. Our previous experience demonstrated that in summer in a greenhouse without airconditioning it is extremely difficult to prevent overdrying in small (100 cm^3) soil samples. Therefore, 50 samples originating from one 25 m^2 plot were pooled into one 5000 cm^3 mixed soil sample. Soil samples were placed in 0.1 $m^2 \times 7$ cm containers. Seedling emergence was observed over two vegetation seasons. Samples were left for winter in an unheated greenhouse. Observation of seedling emergence was carried out every 2-3 weeks. After identification and counting seedlings were removed, and then the soil in the containers was mixed thoroughly to enable the germination of seeds buried in deeper layers.

Data analysis

The total area of collected soil samples for each study site was 2 m^2. The density of seedlings per m^2 did not therefore have to be approximated based on the mean density calculated for small samples. The Shannon-Weiner diversity coefficient H' and Sørensen floristical similarity index *S* were calculated for seed banks from the studied sites and the two sampling dates [27]. The calculations of the *S* coefficient between the seed bank and ground layer omitted bryophytes and lichens encountered in the ground layer.

The correlation between the age of fallow land and seed bank characteristics: number of species (*Sp*), number of diaspores m^{-2} (*N*) and species diversity index of the seed bank (d_1) – where $d_1 = S/lnN$, was studied using regression analysis [28]. The seed longevity index (*LI*) was calculated for each species present in the seed bank using formula proposed by Bekker et al. [29] as follows: number records listed in Thompson et al. [30] data. *LI* = short-term persistent + long-term persistent/transient + short-term persistent + long-term persistent.

Names of flowering plants according to Mirek et al. [31]. Names of bryophytes according to Wójciak [32].

Results

In 1980 the share of the diaspores of dwarf shrubs in the seed bank of the 26-year fallow land was still very low (approx. 5%). The seed bank was dominated by grass and perennial diaspores (each about 33%), and the diaspores of annuals and biennals had about a 10% share (Fig. 1a). Numerous gaps in the ground layer enabled the diaspores of pioneering trees and shrub species to penetrate the soil seed bank, and they had the highest share at this succession stage (approx. 15%). In the following years specimens of *Calluna vulgaris*, spreading and fruiting each year, enriched the seed bank with their diaspores. From among seedlings that emerged from the samples of the seed bank collected from the same site in 1993 and 2004 seedlings of *Calluna vulgaris* constituted as much as 85-90% (Fig. 1a). The structure of the seed bank of *Peucedano-Pinetum* coniferous forest is characterized by the highest share of perennials, a high share of grasses and a very low share of dwarf shrubs in comparison to the previous pre-forest stage. At this stage their penetration to the soil seed bank is insignificant (low rate of cover and frequency of *Calluna vulgaris* in the ground layer = low seed fall) and is additionally hindered by the compact bryophyte layer. Early successional annual species (*Spergula morisonii*, *Conyza canadensis*) are still present in the seed bank but are represented only by single diaspores (Tab. 1). Single diaspores of ruderal annuals (9 species) representing, e.g. genera *Polygonum* and *Fallopia* were also present, which was undoubtedly caused by the proximity of a forest road in use.

The share of early succession species in seed banks

Species present in the seed banks of fallow lands were divided into groups distinguishing succession stages on abandoned fields (according to Faliński [24]). The initial stage was distinguished by species from two groups: annual-biennial segetal and fallow species (A); perennial psammophilous grassland species (B; Tab. 2). In the subsequent, optimal stage

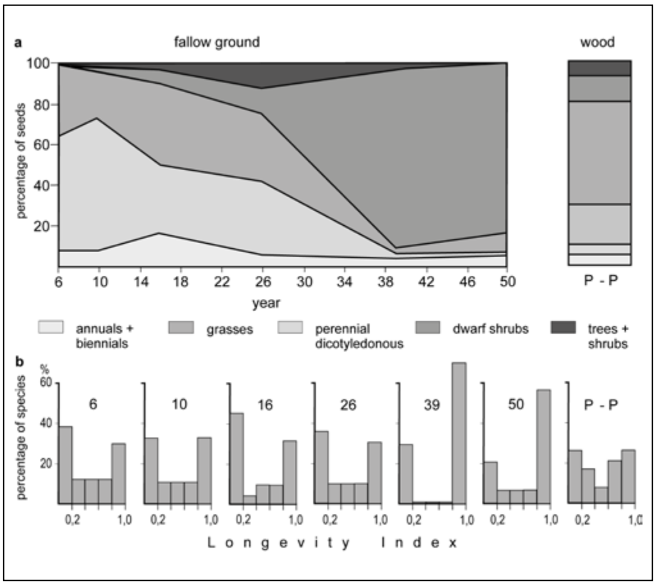

Fig. 1 **a** The share of diaspores of selected species in the seed bank of fallow land aged 6-50 years and of fresh coniferous forest. **b** Distribution of Longevity Index for species forming the seed bank of fallow lands and fresh coniferous forest.

species from the first group withdraw, and *Calluna vulgaris* occurs in the ground layer.

In comparison to the number of species encountered in the seed bank of fallow lands, the number of species distinguishing the initial stage accounts for 60% to 30% of species.

The diaspores of species distinguishing the initial succession stage are continuously present in the seed bank of fallow lands (from 6 to 50 years) but their density varies significantly. On fallow lands aged 6-26 years the diaspores of species from group A and B account for 75-82% of the seed bank, and later their share considerably decreases. On fallow lands aged 39-50 years a high number (approx. 80%) of diaspores originates from one preforest species (*Calluna vulgaris*), which in the fresh coniferous forest *P-P* accounts for only 16% of the seed bank.

Correlation between time and species diversity, density and persistence of seed banks of poor soils

The correlation between the number of species in the seed bank and species diversity (d_1) and time conforms with a statistical model of linear regression (respectively: $y = -0.95x + 57.20$ and $y = -0.09x + 5.71$). The value of both dependent variables decreases in proportion to the time elapsed from the cessation of farming (Fig. 2). In both cases the variable x explains over 80% of demonstrated variation ($r^2 > 0.80$).

The correlation between seed bank density and time is not linear and is described by the exponential regression model. After logarithmic transformation the density values are described by the formula: $lny = -0.05x + 10.3$ and r^2 in this case is higher than 0.90 (Fig. 2).

For the first ten plus years following the cessation of farming the share of annual and biennial species in the seed bank increases relatively quickly, and decreases gradually later. Single diaspores of these species can be found, even in the seed bank of undisturbed coniferous forest (Tab. 1). A different process concerns the share of tree and shrub diaspores which “drop out” from the seed bank when the share of *Calluna vulgaris* increases in the ground layer (and in the seed bank).

Tab. 1 Seed bank of *Peucedano-Pinetum*.

	Seed bank (m^{-2})		
Species	**Σ**	**0-5 cm**	**5-10 cm**
Only in the seed bank			
Betula pendula	118.5	93.0	25.5
Campanula patula	0.5		0.5
Carex arenaria	68.0	44.5	23.5
Carex sp.	5.5	5.5	
Cerastium holosteoides	1.0	1.0	
Conyza canadensis	9.5	9.5	
Epilobium lamyi	1.5	1.0	0.5
Fallopia convolvulus	1.0	1.0	
Frangula alnus	1.0		1.0
Iris sibirica	2.0	1.5	0.5
Juncus bufonius	13.5	6.5	7.0
Oenothera biennis	1.0	0.5	0.5
Plantago media	5.0	3.0	4.0
Poa sp.	3.5	0.5	3.0
Poaceae	110.0	1.0	109.5
Polygonum aviculare	1.5	1.5	
Polygonum hydropiper	1.0	0.5	0.5
Polygonum persicaria	0.5	0.5	
Pulsatilla patens	0.5	0.5	
Ranunculus flammula	1.0		1.0
Senecio vernalis	0.5	0.5	
Sonchus oleraceus	1.5	1.5	
Spergula morisonii	0.5	0.5	
Stellaria media	10.5	1.5	9.0
Taraxacum ofiicinale	4.5	3.0	1.5
Trifolium repens	9.0	8.5	0.5
Urtica dioica	2.5	0.5	2.0
n.n.	1.0	1.0	
In seed bank and vegetation			
Achillea millefolium	3.0	2.5	0.5
Agrostis capillaris	291.5	290.5	0.5
Calamagrostis arundinacea	355.0	257.5	97.5
Calluna vulgaris	226.0	226.0	
Carex digitata	3.0	2.0	1.0
Chamaecytisus ratisbonensis	18.0	16.5	1.5
Deschampsia caespitosa	1.0	0.5	0.5
Erigeron acris	2.5	1.5	1.0
Festuca ovina	6.0	4.0	2.0
Fragaria vesca	0.5	0.5	
Genista tinctoria	0.5	0.5	
Gnaphalium sylvaticum	2.0	1.5	0.5
Hieracium pilosella	3.0	2.5	0.5
Hieracium umbellatum	1.5	1.5	
Hypericum perforatum	45.0	40.5	4.5
Linaria vulgaris	0.5	0.5	
Luzula pilosa	4.0	4.0	
Malus sylvestris	0.5	0.5	
Melandrium album	3.5	1.5	2.0
Picea abies		0.5	
Poa angustifolia	3.0	3.0	
Prunella vulgaris	0.5	0.5	
Rubus idaeus	2.5	1.0	1.5
Rumex acetosella	20.5	11.0	9.5
Solidago virgaurea	0.5	0.5	
Veronica chamaedrys	13.0	5.0	8.0
Veronica officinalis	105.0	67.0	38.0

Tab. 1 *(continued)*

Species	Seed bank (m^{-2}) Σ	0-5 cm	5-10 cm
Vicia cracca	9.5	9.5	
Viola riviniana	16.5	13.5	3.0

Tab. 2 Number of species and density of diaspores in the seed bank of fallow lands aged 6-26 years (based on data by Symonides [8]) and 39- and 50-year-old coniferous forest *Peucedano-Pinetum* (authors' own data).

Age of fallow lands	6	10	16	26	39	50	P-P
Number of species	61	41	37	34	12	17	56
Seed bank density (ca. m^{-2})	30000	24000	15000	6000	3500	3000	1500
Number of species (a + b)	7	6	6	5	2	4	3
Number of species (ppg)	13	14	13	14	2	6	4
Number of species (p-f)	1	3	4	3	1	1	2
% seeds (a + b)	15	19	19	11	5	6	0.3
% seeds (ppg)	61	63	56	67	7	9	5
% seeds (p-f)	0.1	1.5	4.5	6	81	80	16

Ecological groups of species distinguished by Faliński [24]. (a + b) – annual + biennial segetal and fallow species; (ppg) – perennial psammophilous grassland species; (p-f) – pre-forest species.

During the 10 years after cessation of farming, the initially high (>40%) share of grasses and perennials gradually decreases (respectively: $y = -0.76x + 43.38$; $r^2 = -0.761$ and $y = -1.53x + 65.41$; $r^2 = -0.925$). In the following period the correlations are non-linear. In the fresh coniferous forest (*P-P*) seedlings of both plant groups have a high share, and in total account for approx. 75% of the bank size. The share of *Calluna vulgaris* diaspores in the seed bank increases exponentially for the first 40 years ($lny = 0.16x - 1.65$; $r^2 = 0.862$), but later decreases over time and becomes insignificant in the fresh coniferous forest.

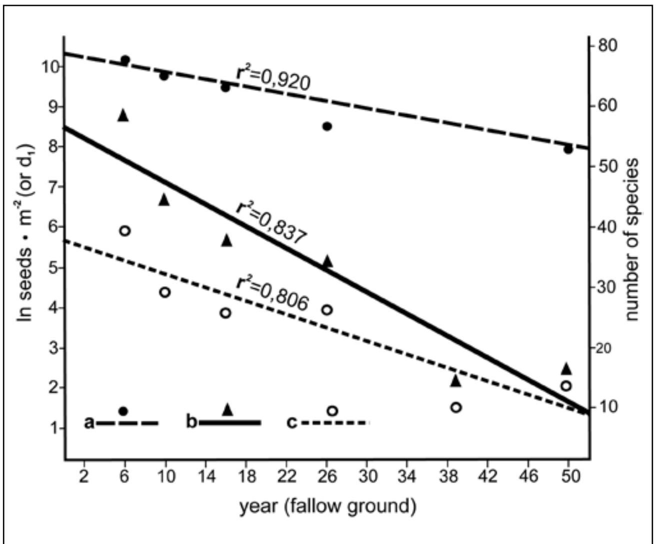

Fig. 2 Relations between species diversity. **a** Species diversity index d_1. **b** Number of species in seed bank. **c** Seedling density/m^{-2} and time of the studied fallow land.

The persistence of the seed banks of different age fallow lands

The values of *LI* were divided into 5 classes (Fig. 1b). The first (*LI* 0-0.2) covers species producing short-lived diaspores, the last (*LI* 0.8-1.0), covers species forming persistent seed banks (Fig. 2). For 25 years from the cessation of farming species from the last group form about 1/3 of the species group present in the soil seed bank. For the first 16 years the seed bank is dominated by species not forming persistent seed banks. However, their number decreases in time. *Calluna vulgaris* spreads out in the ground layer of the 26-year-old fallow land covered with juniper shrubs, pine and aspen brushwood. Gaps between dwarf shrubs are filled in by dense bryophytes and lichens, which makes the penetration of soil by diaspores difficult. Thirteen years later on the same fallow land, in the seed bank of low diversity, mainly species forming persistent seed banks remained (70%). Within the following 11 years trees in some places shade the surface and cause deletion of heliophilous species, including some *Calluna vulgaris* dwarf shrubs, bryophytes and lichens. This process enables the penetration of soil by diaspores of new species, which results in the increase of species diversity of the seed bank and the higher share of species producing seeds of various longevity. The seed bank of fresh coniferous forest (*Peucedano-Pinetum*) is formed by a full spectrum of species producing diaspores of various longevity and none of the *LI* classes reaches a maximum.

The mean value of the longevity index for diaspores increases during succession on abandoned fields (Fig. 3a) whereas the variance coefficient decreases (Tab. 3).

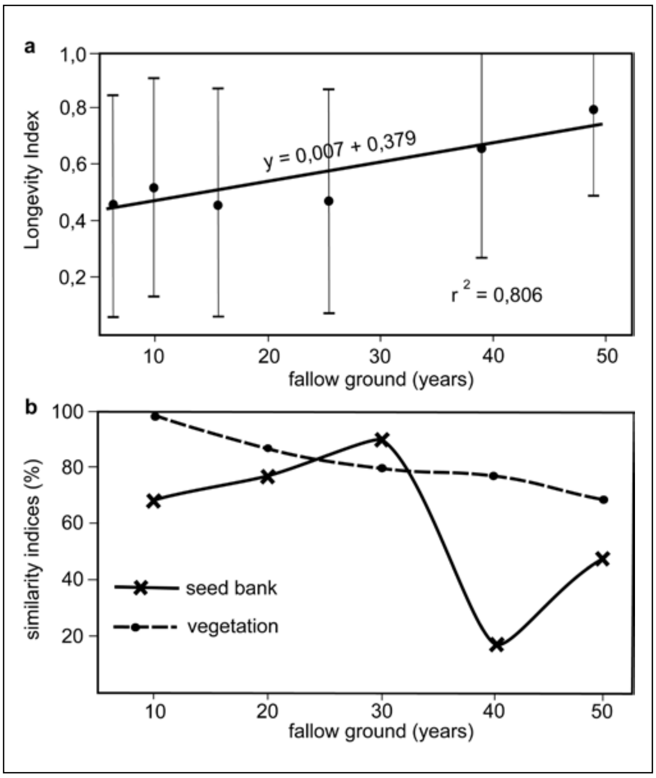

Fig. 3 **a** Correlation between mean *LI* and time. **b** Floristical similarity of the ground layer for subsequent phases and seeds banks of these phases (phases aged 10/6; 16/10; 26/16; 39/26; 50/39).

Tab. 3 Mean, standard deviation and coefficient of variation $V = s/\bar{x}$ Longevity Index for species forming the seed bank of 6-50-year fallow land and *Peucedano-Pinetum* (*P-P*).

Age of fallow lands	6	10	16	26	39	50	*P-P*
	0.463	0.506	0.456	0.472	0.655	0.807	0.529
SD	±0.388	±0.383	±0.409	±0.393	±0.414	±0.291	0.337
$V = s/\bar{x}$	0.840	0.760	0.900	0.830	0.630	0.360	0.640

SD – standard deviation; $\bar{x}$ – mean.

In the last studied decade (40-50 years) the seed bank is formed by species producing the long-lived diasporas. The analysis of floristical similarity for consecutive phases demonstrates a gradually decreasing similarity index for plant cover (Fig. 3b). Changes in the species composition of the seed bank are de-scribed by another pattern. During the first 26 years the similarity of seed banks for consecutive phases increases (the bank is predominantly formed by the species fruiting on the surface). After about 40 years following the cessation of farming a rapid floristical restructuring of the seed bank occurs, associated with the formation of woodstand and the bryophyte layer. In the highly diverse seed bank of the old coniferous forest, early successional species are practically no more present and the seed bank is formed by a completely different species group in comparison to the initial succession phases.

Discussion

The results of our study only partly confirmed the generalisation proposed by Bossuyt and Hermy [18]. In fact, for the first 25 years from the cessation of farming on poor soils in the seed bank there is, among others, a constant group of about 20 early succession species. It is formed by annual and biennial segetal and fallow species (e.g. *Euphorbia stricta*, *Festuca rubra*, *Spergula morisonii* and *Teesdalea nudicaulis*), and perennial psammophilous grassland species (e.g. *Corynephorus canescens*, *Agrostis tenuis*, *Hieracium pilosella*, *Helichrysum arenarium*, *Jasione montana*, *Knautia arvensis* and *Solidago virgaurea*). Their density and number in the soil seed bank rapidly decrease after about 40 years following cessation of farming. During that period the vegetation of the fallow land is dominated by dwarf shrubs, and tree individuals reach the layer of trees and shrubs. Trees (pine and poplar) and shrubs (juniper) play an important role on the 26-year-old fallow land. Their presence radically changes light conditions on the surface and disables the replenishment of the decreasing density of diaspores in the seed bank of early succession species. In poorly diversified seed banks of 40-50 year-old fallow lands only a low number of diaspores of early succession species survived. During that period the soil seed bank is dominated by diaspores of *Calluna vulgaris*, which occur on 10-year-old fallow land [8]. When dwarf shrubs reach the generative phase, the reserve of their seeds in the soil begins increasing. Despite the physiognomical similarity between young pine-aspen forests and old fresh coniferous forest, the composition of the soil seed banks of these communities is very different for qualitative and quantitative aspects. Therefore, it cannot be claimed that the species composition of the seed bank in the entire succession series is relatively constant. The studied case shows that it is true only for the initial stage of secondary succession on poor soils. The restoration of a multi-species ground layer and seed bank restructuring require a considerably longer time than half a century. According to Faliński [24] approx. 200 years is required to restore the community of *Peucedano-Pinetum*. Nevertheless, the question if 200 years is enough time for recreating the seed reserves in soil characteristic for stable, ancient *Peucedano-Pinetum* forest is still opened.

Studies by Fyles [33] demonstrated that the density of diaspores in the seed bank of northern forests depends on the community type, and ranges between approx. 350 and approx. 680 seeds per square meter. Data obtained by us for an undisturbed fresh *Peucedano-Pinetum* coniferous forest show higher density of seed bank amounted 1500 seeds/m^{-2}. All types of Białowieża forest are characterized by very high species abundance and high floristical similarity of the seed bank and ground layer [10,16,27,34].

The similarity between species composition of subsequent phases of vegetation during succession on fallow land decreased with time. However, the process of change in the seed bank is more complicated. For the first 30 years the similarity of seed banks of fallow land gradually increases. After that period pines are recruited to the canopy layer, which entirely changes the surface conditions and decreases the size of the seed fall of pioneering heliophilous species to the seed bank. That period is followed by a gradual "construction" of the coniferous forest seed bank, in which pioneering species are practically absent.

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