

## THE EFFECTS OF DIFFERENT TYPES OF WOODSTAND DISTURBANCE ON THE PERSISTENCE OF SOIL SEED BANKS

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### ABSTRACT

The research was conducted on four patches of thermophilous oak wood in Białowieża Primeval Forest: A – with a woodstand: oak + approx. 30-year-old hornbeam + hornbeam brushwood; B – with a hornbeam stand formed by natural seed fall after logging (ca. 1920) oaks; C – after logging oaks and replanted (ca. 1965) with pine and oak; D – with a natural low-density oak stand. Species composition and seed bank density were estimated using the seedling emergence method. Seedling emergence was observed over two vegetation seasons. Research demonstrated that: 1) the species abundance of the seed banks depends on canopy cover (A, B approx. 50 species; C, D approx. 70 species); 2) the floristical similarity (Sørensen's index) of the seed bank and ground vegetation is higher in the undisturbed patch D (0.50) than in disturbed patches (0.30-0.35); 3) species diversity in plots A, B, C, D ( $H^2=12.5; 13.4; 15.5; 16.9$ ) and seed bank density per m<sup>2</sup> (432.5; 958.0; 1486.5; 2268.0) are negatively correlated with the degree of patch shading; 4) the average weight of diaspores in the seed banks of shady plots is lower (A, B approx. 0.003 g) than that of sunny plots (C, D approx. 0.08 g); 5) the share of long-lived diaspores increases in patches after logging.

KEY WORDS: density; disturbance; frequency; longevity index; persistence; soil seed bank.

### INTRODUCTION

The *Potentillo albae-Quercetum* community is the only thermophilous forest in Białowieża Primeval Forest. The characteristic composition of species in this community covers a wide ecological spectrum of species with contrasting demands for light, moisture and trophic conditions (Kwiatkowska 1993). In the Polish part of Białowieża Primeval Forest *Potentillo albae-Quercetum* communities have been found only on the plateau and the southern slopes of moraine and kame hills, and they are surrounded by shady hornbeam forest *Tilio-Carpinetum* (Kwiatkowska 1986). The area covered by thermophilous oak forest continues to decrease for various reasons. Many thermophilous oak wood habitats were destroyed between World War I and II due to the construction of a railway line and gravel and sand pits. In the same period a number of

thermophilous oak wood patches were destroyed by the logging of woodstands which were precious for economic reasons (Faliński 1986). Over the past forty years the preserved patches have rapidly declined. This process has resulted directly from the invasion of hornbeam into habitats of thermophilous oak wood (Kwiatkowska and Wyszomirski 1988, 1990; Kwiatkowska et al. 1997). Hornbeam invasion resulted from repetitive changes in the type and level of pressure from herbivores (on trees, shrubs and herbaceous plants) in the 18th, 19th and 20th century (Kwiatkowska 1996; Kwiatkowska-Falińska 2006). Hornbeam specimens growing above the ground vegetation layer increase overshadowing of the forest floor and trigger the gradual deletion of species, with speed positively correlated with light demands (Kwiatkowska 1994a). Growing hornbeam brushwood causes the gradual transformation of a thermophilous oak forest patch towards the sur-

rounding Tilio-Carpinetum (Kwiatkowska and Solińska-Górnicka 1993). Currently, in Białowieża Primeval Forest there are no thermophilous oak forests with natural woodstands and diversified ground vegetation formed by numerous heliophilous species (Kwiatkowska 1996). The soil seed bank, defined as a pool of seeds with germinating potential present in the soil, is considered a type of “evolutionary memory” for the plant community, preserving past events (Harper 1977). Even with clear logging the previously deposited seeds are able to survive in the soil. When conditions are suitable for diaspore germination, the seed bank may play a significant role in the restoration of the community (Kwiatkowska and Solińska-Górnicka 1993). However, there is a common opinion in the literature that the species composition in the seed bank of forest communities demonstrates low similarity to ground vegetation (Pickett and McDonnell 1989; Thompson 1992; Dölle and Schmidt 2009; Wódkiewicz and Kwiatkowska-Falińska 2010a, 2010b). In addition, some authors claim that the low-abundance and diversified seed bank of forest communities is dominated by heliophilous species, typical for early succession stages. These species demand a large amount of light, both for germination and further development (Thompson and Grime 1979). However, the results of research conducted in Białowieża Primeval Forest have not confirmed these conclusions. Floristical similarity between the ground vegetation and the seed bank both in undisturbed and disturbed Tilio-Carpinetum communities is high (70%) (Jankowska-Błaszczuk et al. 1998; Panufnik-Mędrzycka and Kwiatkowska-Falińska 2001). In Tilio-Carpinetum communities it attains similarly high values, both in a patch with natural woodstand and that which formed spontaneously 90 years following logging (Jankowska-Błaszczuk and Grubb 1997). In the discussed communities species abundance was also high. The observation of seedling emergence conducted over one vegetation season demonstrated 45 species in the seed bank of Tilio-Carpinetum and 51 species in that of Potentillo albae-Quercetum (Jankowska-Błaszczuk et al. 1998). These groups of species included a high number (approx. 30%) of ancient forest species. The main disturbance factor in forest communities is the rapid natural or anthropogenic increase in the access of the full light spectrum to ground vegetation.

The seed bank of the Tilio-Carpinetum patch with a secondary woodstand demonstrated a higher share of heliophilous species than the patch with natural woodstand. However, these species do not represent early succession stages, but a strategy of waiting for large-scale disturbances of the tree canopy. For germination they require access to the full light spectrum (Jankowska-Błaszczuk and Grubb 1997; Jankowska-Błaszczuk and Daws 2007). In forests with highly shaded ground vegetation, such as Tilio-Carpinetum, the seed bank is enriched with heliophilous species which grow in gaps in the first year during the process of gradual gap filling. The increased size of the seed bank by species from taxa: *Urtica*, *Hypericum*, *Juncus* provides clear information about past disturbance (Jankowska-Błaszczuk and Grubb 1997). It should be assumed that in Potentillo albae-Quercetum communities, characterised by good access of light to the ground vegetation layer, clearing trees probably less significantly changes the size and diversity of the seed bank than disturbances

caused by increased shading of the forest floor by invading hornbeam trees.

The objective of the study was to analyse the effects of logging and hornbeam recruitment in oak forest on floristical similarity of the seed banks and vegetation and on seed banks diversity and density. Logging is expected to increase diversity and density of seed banks, while hornbeam recruitment is expected to have opposite effect. We hypothesise also that both types of disturbances should decrease similarity between seed bank and vegetation.

#### *Study area and characteristics of study sites*

The study was conducted on four 480 m<sup>2</sup> permanent plots (objects: A, B, C, D) located in the central part of the Polish fragment of Białowieża Primeval Forest. Plots A, B and D were located in a landscape reserve and plot C was established in the area of production forests.

Object A – research site located in forest district 442B. It covered a fragment of a thermophilous oak wood patch strongly transformed by approx. 30-year-old hornbeam, physiognomically similar to floristically low-diversified Tilio-Carpinetum with a high share of juvenile hornbeams in the shrub layer (50%). *Carpinus betulus* was a dominant woodstand species, and was accompanied by *Quercus robur* and *Picea abies*. Trees-cover in this patch was 80-100%, and the ground vegetation cover was very low, not exceeding 20%. The mean number of species per 100 m<sup>2</sup> was 25. The majority of species were characteristic for deciduous forests.

Object B – research site located in forest district 386A. It covered a fragment of thermophilous oak wood patch at an advanced stage of decline. The patch was physiognomically similar to Tilio-Carpinetum typicum. In the 1920s a natural oak forest had been logged and the current tree stand formed spontaneously from natural seed fall. The shrub layer was poorly developed (10%). The woodstand was dominated by hornbeam, with an admixture of birch, spruce and oak. The canopy cover was high (70-80%), while the ground vegetation cover demonstrated relatively low diversity (on average 39 species per 100 m<sup>2</sup>). The vegetation cover was 40-50%.

Object C – research site located in forest district 543C. It covered a fragment of thermophilous oak wood patch on a slope and plateau of a kame hill. In the 1960s a natural oak forest had been logged and the soil ploughed prior to planting of *Pinus sylvestris* and *Quercus robur*. During the study a low canopy cover woodstand (30-50%) was dominated by restoring pine, with an admixture of oak, hornbeam and spruce. The vegetation was relatively rich (on average 77 species per 100 m<sup>2</sup>) and luxuriant. It covered 60-80% of the plot and was characterised by a high proportion of heliophilous species.

Object D – research site located in forest district 442B. It covered a fragment of a previously extensive patch of thermophilous oak wood (the same as in plot A). In this part hornbeam invasion has only just begun, and its juvenile specimens were not higher than the ground vegetation. The tree layer was formed by old oaks. Canopy density was below 45%. Luxuriant, rich ground vegetation has survived here, (on average 82 species per 100 m<sup>2</sup>) covering 80% of the plot. The species composition and structure of the ground vegetation was typical for Potentillo albae-Quercetum.

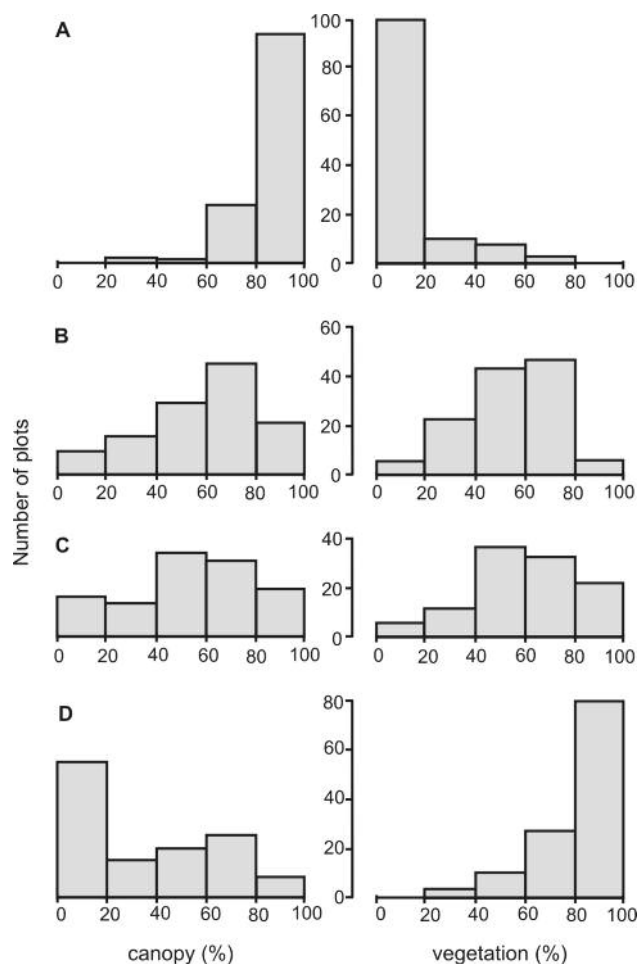


Fig. 1. Canopy and vegetation cover (%) in research objects (A-D).

#### Characteristics of light conditions in the study area

Research plots were characterised by significant differences in the access of light to the forest floor, both for a modal value of canopy density and in the proportion of strongly shaded plots (Fig. 1). In plot A almost all subplots were strongly shaded (canopy density >80%) by hornbeam, which in this plot formed the woodstand  $A_2$  and is encountered in brushwood. In plot B an old hornbeam stand, in which maximum of the process of natural selection of trees is over, strongly shades about 50% of the area. Small gaps have formed between tree crowns. In plot C fairly strong (>50%) shading concerns a half of the subplots, but, apart from numerous gaps in the canopy, the light penetrates to the forest floor via open-structure pine crowns. The highest number and area of gaps was found in plot D, where almost a half of the plots are only 20% shaded. The rate of cover for ground vegetation depends on access to light. On the most shaded subplots and plots the rate is very low (<20%), and it is very high in places with good access to light (Fig. 1).

#### Field sampling

In each of the four 480 m<sup>2</sup> plots (12×40 m) 120 subplots were established (2×2 m). In summer 1997 species of vascular plants were surveyed on each plot, and the rate of cover for ground vegetation as well as for canopy were calculated.

Samples were collected for the analysis of the soil seed bank in early spring 1997 from a transect (2×40 m) located

within the research plots. Litter covering mineral soil was removed prior to sample collection. Soil cores from each 2×2 m plot were collected with an open-ended soil probe (100 cm<sup>3</sup>) to obtain a 6000 cm<sup>3</sup> total sample volume for each subplot. Afterwards, each soil sample was separately sorted to remove underground plant parts and gravel. A 4000 cm<sup>3</sup> sample was collected from the remaining soil and placed in 0.1 m<sup>2</sup>×7 cm containers.

#### Greenhouse procedure

The species composition and seed bank density were determined using the seedling emergence method (Ter Heerd et al. 1996; Leck et al. 1989). The containers were kept in an unheated greenhouse, where the temperature in winter was below 0°C. Seedling emergence was observed over two vegetation seasons (until November 1998). When necessary, samples were watered with distilled water to maintain constant soil humidity. After identification and counting, seedlings were removed, and then the soil in the containers was stirred thoroughly to enable the germination of diaspores from deeper layers.

#### Data analysis

Frequency of ground vegetation species for objects was calculated based on their frequency of occurrence on 120 subplots. Frequency of species in the seed bank was calculated based on the occurrence of species in 20 soil samples.

Species diversity in ground vegetation and seed bank for individual plots was calculated based on the Shannon-Weiner diversity coefficient:  $H' = -\sum p_i \ln p_i$ ; where  $p_i$  was calculated based on the frequency of species in the ground vegetation and seed bank.

Floristical similarity between the species in the seed bank and ground vegetation was calculated using the Sørensen similarity index (Sørensen 1948; Hopfensperger 2007).

For the seed bank of each objects the following characteristics were calculated: number of species in the total samples, average number of species ( $\bar{x}$ ), standard deviation (SD) per 0.1 m<sup>2</sup> and  $\bar{x}$  number of seedlings  $\pm$  SD per 0.1 m<sup>2</sup>.

The persistence of soil seed banks was estimated based on the longevity index (LI), which for persistent seed banks has values from 0 to 1. Literature data (Thompson et al. 1997) for the calculation of LI were found for 88 species. Mean values of LI and SD were calculated based on them for each objects.

The seed longevity index (LI) was calculated for each species found in the seed bank using a method by Thompson et al. (1997) and Bekker et al. (1998, 1999).

The significance of differences between the average values was analysed with the *t*-Student test (Sokal and Rolf 1981). The comparison of mean LI and mean particular of objects (A, B, C, D) was also conducted based on the standardized variable  $u = (\bar{x}_i - \bar{x}) / SD$ , where  $\bar{x}_i$  – mean for species in the seed bank of the individual plot,  $\bar{x}$  – mean for all species encountered in the seed banks of four objects.

## RESULTS

#### Similarity and species diversity of the ground vegetation and seed bank

The studied objects demonstrated low similarity of species composition in the ground vegetation (Table 1).

TABLE 1. Value of Sørensen's index of similarity between particular objects (A-D) regarding the seed banks and ground vegetation.

		Seed bank			
		A	B	C	D
Vegetation	A	×	60.7	52.8	58.1
	B	37.7	×	61.4	55.6
	C	38.4	49.4	×	53.7
	D	40.3	48.4	63.0	×

Values of the floristical similarity index  $S$  calculated for all paired plots range within approx. 40-60%. The closest similarity ( $S=63.0\%$ ) was demonstrated for plots C and D. Both plots were characterised by low-density woodland,

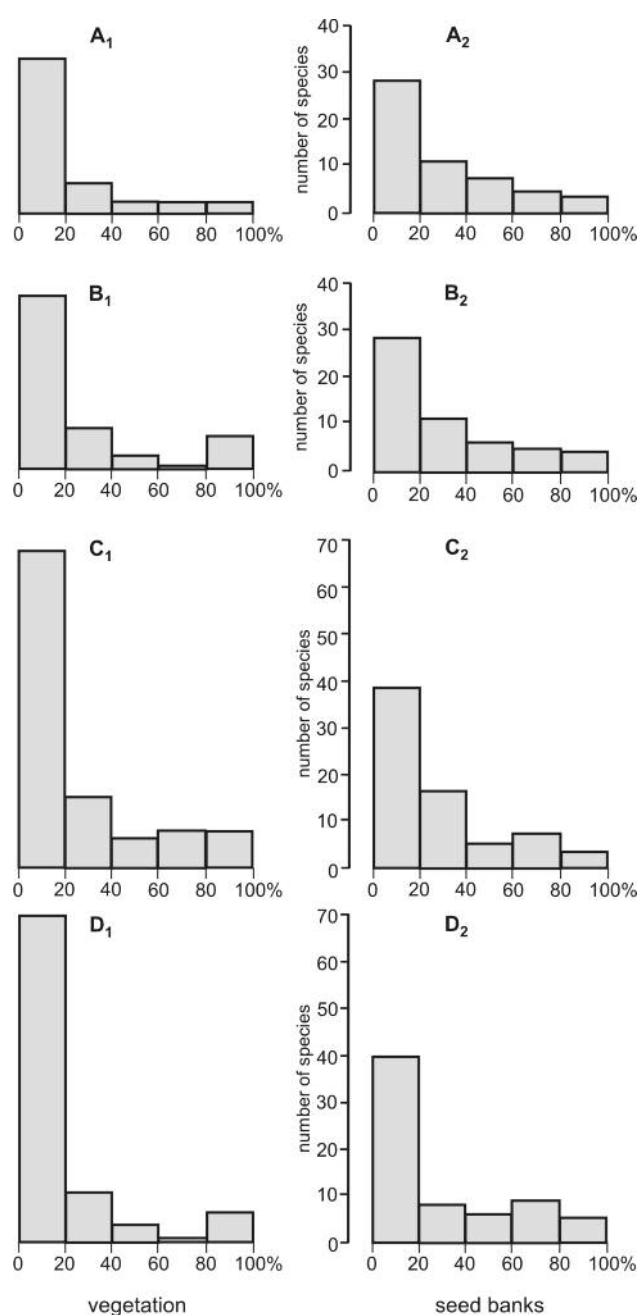


Fig. 2. Frequency of species in the vegetation ( $A_1$ - $D_1$ ) and in the seed banks ( $A_2$ - $D_2$ ) of research objects.

which allowed for the penetration of large amounts of light to the ground vegetation (Fig. 1).

On the study plots both species diversity and the above ground vegetation cover were negatively correlated with canopy density. In plots C and D the number of species was least two times higher than in the strongly shaded plots, A and B. In total, 159 taxa were encountered on four plots, including 47 ancient forest species. In all plots low-frequency species (<20%) had the highest share. High-frequency species in a plot (80-100%) had a very low share (Fig. 2).

The seed banks of individual plots demonstrated higher floristical similarity to each other than the ground vegetation.  $S$  values range in a twice lower spectrum (50-60%). The closest similarity between seed banks was demonstrated for plots B and C ( $S=61.4\%$ ), which have been formed over several dozen years following logging (Table 1).

The analysis of all samples of soil seed bank demonstrated the presence of 125 taxa, of which 95 were also present in the ground vegetation. Species abundance of the seed banks in individual plots ranged within a more narrow spectrum (min. 50, max. 70 species) than in the ground vegetation (min. 53, max 116). In both cases ancient forest species were present in the plots. Low-frequency species (<20%) dominated in the seed bank of all plots (>50%). The structure of species from different frequency classes in the seed bank was slightly more balanced than in the ground vegetation (Fig. 2). In both cases J-shaped histograms were obtained.

The diversity coefficients (number of species in a plot and value of  $H'$  coefficient) calculated for the ground cover and seed bank classified plots A, B, C, D in a similar manner from the least diversified A to the most diversified D (Table 2). Values of the  $H'$  coefficient calculated for ground vegetation classified plots into two groups: A and B ( $H'=7.2$  and  $H'=8.4$ ) and C and D ( $H'=19.6$  and  $H'=18.7$ ). Values  $H'$  calculated for the seed banks of individual plots were less diversified than for the ground vegetation (Table 2).

Floristical similarity between seed banks and vegetation in plots A, B, and C was low ( $S$  index approx. 30%). The seed bank of plot D, with the least disturbed woodland structure, demonstrated the closest floristical similarity to the ground vegetation ( $S=49.1\%$ , Table 2).

#### Persistence of seed bank and weight of diaspores

Analysis of persistence was conducted for a group of species for which information for the calculation of LI was available and the weight of seeds was known (Table 3). For that reason the analysis was performed for a lower number of species: (A=46/55; B=45/57; C=52/70; D=58/69; a denominator indicated the number of species found in the seed bank of a particular plot).

We assumed that the seed banks formed by long-lived species would have a higher mean LI than the banks dominated by short-lived diaspores. Therefore, our assumption was that in plots A and B, invaded by hornbeam for over 30 years, the seed banks would contain the diaspores of species forming persistent seed banks. Thus, the mean LI for plots A and B should be higher than the mean LI calculated for C and D. No statistical proof ( $t_1 > t_0$ ) for this hypothesis was obtained owing to the high variability of LI. However, mean values expressed as standardized variable  $u$  categorized plots into two groups: never logged (A

TABLE 2. Characteristics of the seed banks of research plots.

Seed bank	A	B	C	D
Number of species	55	57	70	69
$\bar{x}$ number of species 0.1 m <sup>2</sup>	12.4±2.7	13.0±3.8	21.5±6.6	20.7±4.8
$\bar{x}$ number of seedlings 0.1 m <sup>2</sup>	43.3±45.8	95.8±37.0	74.3±35.3	73.4±35.6
$\bar{x}$ number of seedlings 0.1 m <sup>2</sup> L=0, 1, 2	2.6±1.0	0.9±0.7	1.1±0.9	2.1±1.2
$\bar{x}$ number of seedlings 0.1 m <sup>2</sup> L=3, 4, 5	3.0±1.4	3.1±1.8	4.3±2.5	5.8±2.0
$\bar{x}$ number of seedlings 0.1 m <sup>2</sup> L=6, 7, 8	5.7±2.0	7.4±2.4	14.5±4.0	12.1±3.2
Shannon's index H'	12.5	13.4	15.5	16.9
Sorenson's index (seed bank/vegetation)	34.8	31.3	30.3	49.1
Longevity index	$\bar{x}$ 0.433 SD 0.344	0.464 0.348	0.471 0.330	0.396 0.358
Weight of seed	$\bar{x}$ 0.003 SD 0.008	0.003 0.007	0.084 0.562	0.079 0.539

and D) and logged B and C (Fig. 3). The distribution of LI for all plots is bimodal (Fig. 4) and highly variable (SD close to  $\bar{x}$ , Table 2). The peaks probably correspond with the pool of short-lived (LI=0-0.4) and long-lived seeds (LI>0.6).

When assuming the correlation between the weight of seeds and longevity we expected the mean weight of seeds from the banks of plots A and B to be lower than that of C and D. Such a tendency was revealed when mean values for plots were expressed in units of standardized variable  $u$ .

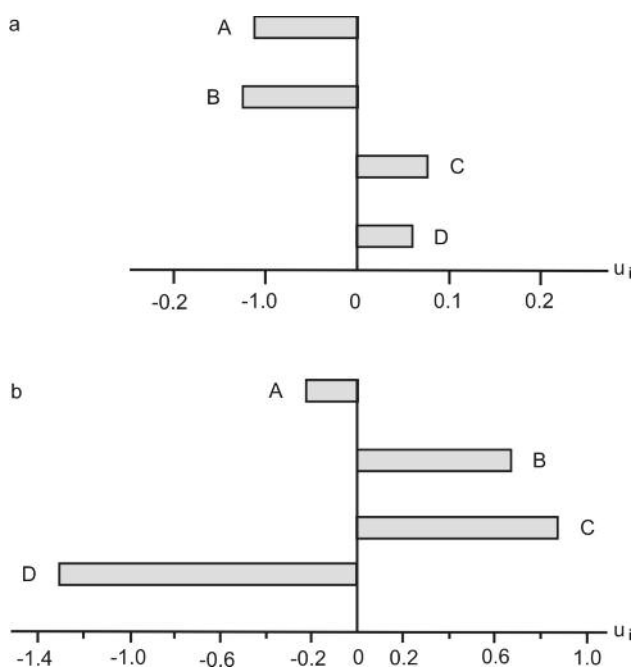


Fig. 3. Mean weight of seeds (a) and mean longevity index (b) expressed in the values of standardized variable "u".

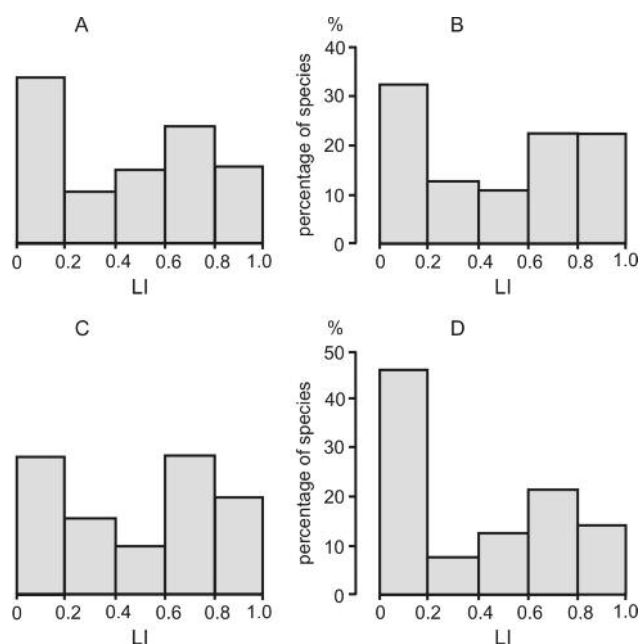


Fig. 4. Distribution of longevity index (LI) in research objects.

## DISCUSSION

A number of publications regarding the discussed subject largely reflect the condition of well-preserved natural forest complexes in Europe and, on a smaller scale, in the North America. Białowieża Primeval Forest, which has been uninterruptedly covered by deciduous forest for thousands of years, is for this reason the only model of natural temperate deciduous forest (Boussuyt and Hermy 2001; Fenner and Thompson 2005; Boussuyt and Honmay 2008).

In view of that, the fact that the seed banks of natural temperate deciduous forests are among the poorest studied types of plant communities should not be surprising (Thompson et al. 1997). However, there are a high number of publications concerning other communities found in all geographical zones (e.g. Grime 1989; Vyvey 1989a-b; Thompson et al. 1997; Chang et al. 2001; Fenner and Thompson 2005).

### Seed bank density

A number of papers have focused on the role of seed banks in different plant dynamics processes, such as primary succession (Tsuyuzaki 1991; Grandin and Rydin 1998; Grandin 2001), secondary succession (Donelan and Thompson 1980; Conn et al. 1984; Symonides 1986; Milberg 1992, 1995; Buckley et al. 1997; Falińska 1999; Hyatt and Casper 2000; Bossuyt and Hermy 2004; Wagner et al. 2006), decline (Panufnik-Mędrzycka and Kwiatkowska-Falińska 2001), or regeneration (Jankowska-Błaszczuk 2002). Our study falls within this research mainstream. The analysed communities undergo spontaneous and anthropogenic transformation from sunny *Potentillo albae-Quercetum* to shady *Tilio-Carpinetum*, and changes in seed banks are associated with changes in the ground vegetation. The decline of the extensive thermophilous oak wood patch where plots A and D were located has been well documented (Kwiatkowska 1986, 1993, 1994a, b, 1996; Kwiatkowska and Wyszomirski 1988, 1990; Kwiatkowska and Solińska-Górnicka 1993; Kwiatkowska-Falińska 2006).

TABLE 3. Longevity index (LI), weight of seeds and frequency of species in the seed bank of individual objects (only species for which the calculation of LI was possible are indicated in the table). Asterix denotes the weight of a seed indicates data obtained from our own measurements and based on a low number of seeds.

Species	LI	Weight of seed	Frequency			
			A	B	C	D
<i>Agrostis capillaris</i>	0.66	0.000060	5	50	10	5
<i>Ajuga reptans</i>	0.45	0.001470	50	75	30	75
<i>Anemone nemorosa</i>	0.02	0.001545	65	25		80
<i>Anthriscum ramosum</i>	0	★0.009600		25		
<i>Arabis thaliana</i>	0.83	0.000030			10	
<i>Asteris vulgaris</i>	0.76	0.000120		10		5
<i>Astragalus glycyphyllos</i>	0	0.004540		100	5	50
<i>Betula pendula</i>	0.66	0.000150	100	100	75	95
<i>Calamagrostis arundinaceae</i>	0.25	★0.004400				
<i>Campanula persicifolia</i>	0.5				80	
<i>Campanula rapunculoides</i>	0.67	0.000270				5
<i>Carex digitata</i>	0.17	0.001090		5		
<i>Carex sylvatica</i>	0.67	0.001660	5	25	25	
<i>Carpinus betulus</i>	0	0.041100	100	85	25	100
<i>Chenopodium album</i>	0.91	0.001157		5		5
<i>Conyza canadensis</i>	0.85	0.000050	5	20		20
<i>Dactylis glomerata</i>	0.2	0.000510		10		55
<i>Epilobium montanum</i>	0.57	0.000120	35	5		15
<i>Erigeron annuus</i>	1	★0.000025	30		10	
<i>Fallopia convolvulus</i>	0.83	0.001280			10	
<i>Festuca gigantea</i>	0.1	0.003120				5
<i>Fragaria vesca</i>	0.34	0.000310		20	30	
<i>Galeopsis tetrahit</i>	0.46	0.004830	15	15		75
<i>Galium boreale</i>	0	0.000600				5
<i>Galium mollugo</i>	0.08	0.000710			20	10
<i>Genista tinctoria</i>	0	0.003600	15	25		15
<i>Geranium sylvaticum</i>	0	0.005095				5
<i>Geum urbanum</i>	0.14	0.000730	40	5	5	35
<i>Gnaphalium sylvaticum</i>	1	0.000030	30		70	10
<i>Gnaphalium uliginosum</i>	0.91	0.000070	25	5	10	
<i>Hepatica nobilis</i>	0	★0.153000				5
<i>Hypericum maculatum</i>	0.5	0.000080	15	25	40	15
<i>Hypericum montanum</i>	1	0.000060	25	5	25	50
<i>Hypericum perforatum</i>	0.9	0.000100	20	60	100	15
<i>Juncus effusus</i>	0.95	0.000010	55	75	35	
<i>Knautia arvensis</i>	0.04	0.006700			5	
<i>Lapsana communis</i>	0.95	0.001300				55
<i>Lathyrus niger</i>	0	★0.193400				5
<i>Lathyrus pratensis</i>	0.09	0.013600				10
<i>Lathyrus vernus</i>	0	★0.012900				10
<i>Luzula pilosa</i>	0.75	★0.002900	30	15		25
<i>Lychnis flos-cuculi</i>	0.56	0.000150	15			
<i>Lysimachia nummularia</i>	0.13	0.000500	5			
<i>Lythrum salicaria</i>	0.24	0.000060	10			
<i>Maianthemum bifolium</i>	0	0.009100				5
<i>Medicago lupulina</i>	0.64	0.002000				5
<i>Melanopyrum nemorosum</i>	0	★0.059100				35
<i>Melica nutans</i>	0.14	0.002560				15
<i>Melittis melissophyllum</i>	1	0.005390		10		
<i>Milium effusum</i>	0.2	0.001380				50
<i>Moehringia trinervia</i>	0.69	0.000220	45	60	60	80
<i>Mycelis muralis</i>	0.5	0.000340				5
<i>Origanum vulgare</i>	0.75	0.000100				70
<i>Oxalis acetosella</i>	0.19	0.001000	75	10		30
<i>Plantago major</i>	0.79	0.000165				
<i>Plantago media</i>	0.32	0.000790		5	5	
<i>Populus tremula</i>	0	0.000110		5		
<i>Potentilla erecta</i>	0.44	0.000580	45		5	15
<i>Primula veris</i>	0.08	0.000690	5			15
<i>Prunella vulgaris</i>	0.33	0.000800				5
<i>Quercus robur</i>	0	3.853000				5
<i>Ranunculus lanuginosus</i>	0		15	5	10	35
<i>Ranunculus repens</i>	0.68	0.002060		10	5	
<i>Rubus idaeus</i>	0.66	0.002700	50	40	10	70
<i>Rubus saxatilis</i>	0	0.010300	5			5
<i>Rumex acetosella</i>	0.69	0.000400			40	
<i>Sagina procumbens</i>	0.87	0.000020		20	20	10
<i>Scrophularia nodosa</i>	0.92	0.000110		5		10
<i>Solanum nigrum</i>	0.73	0.000970	5			
<i>Sonchus arvensis</i>	0.96	0.000600		5		5
<i>Stachys sylvatica</i>	0.38	0.001400				
<i>Stellaria graminea</i>	0.35	0.000273	5		10	
<i>Stellaria holostea</i>	0	0.002100	25	55	30	75
<i>Stellaria media</i>	0.75	0.000510	45	10	35	5
<i>Taraxacum officinale</i>	0.3	0.000600	30	10	30	5
<i>Thalictrum aquilegifolium</i>	0	★0.108700	25			10
<i>Tilia cordata</i>	0	0.031000				5
<i>Torilis japonica</i>	0.62	0.001900			5	35
<i>Tridentalis europaea</i>	0.33	0.000680		5		
<i>Trifolium medium</i>	0	0.002340	20			
<i>Trifolium repens</i>	0.4	0.000640	10	35	65	10
<i>Urtica dioica</i>	0.78	0.000200	90	25	15	90
<i>Veronica chamaedrys</i>	0.38	0.000250	75	95	80	90
<i>Veronica officinalis</i>	0.65	0.000110	65	40	30	55
<i>Veronica serpyllifolia</i>	0.72	0.000050	5			
<i>Vicia cracca</i>	0.07	0.014290	25	20	60	40
<i>Vicia sepium</i>	0.04	0.026000	5	5		
<i>Viola riviniana</i>	0	0.001000	90	90	100	100

The density of the seed banks of deciduous forests is affected by forest naturalness, forest size, woodland age, history of patch use and soil type (Bossuyt and Hermy 2001; Bossuyt et al. 2002; Jankowska-Błaszczuk and Grubb 2006). It has been demonstrated that diaspore density in the seed banks of deciduous forest is several times lower than that of open ecosystems. In natural and ancient forest density ranges from about a thousand to a few thousand diaspores per m<sup>2</sup> (Marquis 1975; Petrov and Palkina 1983; Pirożnikow 1983; Petrov 1987; Staaf et al. 1987; Pickett and McDonnell 1989; Matlack and Good 1990; Mladenoff 1990; Jankowska-Błaszczuk et al. 1998; Leckie et al. 2000). Data obtained in this study (seedling emergence method conducted for two vegetation seasons) fall within the same range (plot: C – approx. 1500, D – approx. 2000 seeds per m<sup>2</sup>). A significantly lower seed bank density was found for plots with hornbeam present in the woodland (plot: A – approx. 450, B – approx. 1000 seeds per m<sup>2</sup>). The strongest negative effect of hornbeam on seed bank density was found in plot A, where hornbeam was present in the woodland and brushwood. In plot B (after oak logging) the secondary hornbeam woodland was formed within approx. 80 years, and has already passed the stage of intensive thinning in brushwood layer. It had a lower density than in plot A. The two times higher seed bank density in plot B compared to plot A, depending mainly on the high proportion of diaspores of heliophilous species, is a repercussion of logging (Table 2).

#### *Diversity and similarity of seed banks and vegetation*

The seed banks of natural undisturbed forests in Białołęka Primeval Forest were characterised by an exceptionally high species diversity and close floristical similarity between the ground vegetation and seed bank (Jankowska-Błaszczuk et al. 1998). Diversity in an undisturbed thermophilous oak wood patch (plot D) after the first vegetation season was estimated at 51 species. It increased to 69 species in the second year of observation, when seedlings of 18 species previously absent in the vegetation emerged. This caused a decrease in the similarity index from approx. 70% (reported by Jankowska-Błaszczuk et al. 1998) to approx. 50%. This fact is highly significant for methodological aspects and implies that seedling emergence should be observed for longer than one vegetation season. As demonstrated in our study, a number of species germinate in a greenhouse not earlier than in the second year of observation, which is probably associated with the process of “risk spreading germination” (Grubb 1988).

The soil seed bank and ground vegetation of thermophilous oak forest contains a high number of species of high and moderate light demand, which usually form a long-term persistent seed bank (Jankowska-Błaszczuk et al. 1998; Panufnik-Mędrzycka and Kwiatkowska-Falińska 2001). Hornbeam, over its 30-year invasion period, filled in natural gaps between oak canopies in plot A and formed luxuriant brushwood. In this patch overshadowing of the forest floor resulted in a gradual deletion of species from the characteristic combination in thermophilous oak woods. Heliophilous species were deleted first (Kwiatkowska et al. 1997), and except for three species from genus *Hypericum*, their diaspores did not survive in the soil for as long a time. Despite low similarity between the vegetation in plots A and B ( $S=37.7\%$ ), seed banks of plots with hornbeam

woodstand (formed after logging and spontaneous invasion) demonstrate close similarity ( $S$  coefficient approx. 60%). Heliophilous species have the highest share in the seed bank of these plots, but they are not present in the vegetation of undisturbed thermophilous oak woods. This group contains, for example, numerous anemochoric species not found in the ground vegetation layer. Similar divergence between the share of species in the ground vegetation and seed bank concerns the diaspores of species from taxa *Epilobium*, *Hypericum*, *Juncus* and *Rubus*, whose high number is found in almost all types of forest communities growing in the temperate zone (Olano et al. 2002; Godefroid et al. 2006). The ecological literature defines them as “canopy-gap-demanded species” and they are present in all plots, with particular abundance in the seed banks of communities with a history of clear logging. This process also resulted in the closest floristical similarity, between the seed bank of plots B and C ( $S>60\%$ ).

All the studied communities were present in the same habitat where undisturbed thermophilous oak woods (plot D). The diversity and similarity of seed banks and vegetation was affected by two factors: hornbeam pressure and logging. Whether the woodland with hornbeam was formed by invasion into the habitat of thermophilous oak wood, or the hornbeam cohort invaded the clearing, the long-term pressure of hornbeam on the plant cover caused a decrease in the diversity and floristical similarity of seed bank and ground vegetation. Importantly, after such a long time the diaspores of species typical for thermophilous oak wood are not preserved in the seed bank, and this type of disturbance in the natural woodland disables the restoration of the heliophilous vegetation of *Potentilla albae-Quercetum* from the pool of diaspores present in the soil.

Planting pine on a clear site formed by logging of thermophilous oak wood has opposing consequences. Ploughing retrieves diaspores of thermophilous oak wood species from the deeper layers, so their populations are able to be restored from the pool of diaspores deposited in the soil (Bossuyt and Honnay 2008; Hautala et al. 2008).

#### *Persistence of seed banks*

In our study changes in the seed bank followed changes in the vegetation, which has also been reported by other authors (Bekker et al. 1999) and (Wolters and Bakker 2002). In contrast to the common opinion about the low persistence of seed banks of forest species characterised by low and moderate light demands, their share in the soil seed bank of thermophilous oak wood is relatively constant (Jankowska-Błaszczuk et al. 1998). The presence of shade-tolerant species in the seed banks has also been confirmed by Staaf et al. (1987), Buckley et al. (1997), Boussuyt et al. (2002), and Godefroid et al. (2006).

Findings by Panufnik-Mędrzycka and Kwiatkowska-Falińska (2001) indicate that some heliophilous forest species (e.g. *Betonica officinalis*, *Gnaphalium sylvaticum*, *Potentilla erecta*) preserve their germinating potential for over 10 years. A large group of species of high and moderate light demand forms long-term persistent banks according to a classification by Thompson et al. (1997), with diaspore longevity of over five years.

Jankowska-Błaszczuk and Grubb (2006) emphasized that in the initial period of studies on seed banks, the strategy in which persistent seed banks are formed was only attributed

to species of high light demand. Contrary to the common opinion about the low persistence of seeds of low light demand species (typical for the vegetation of deciduous forests), an increasing amount of data proves their significantly higher share in seed banks (Jankowska-Błaszczuk et al. 1998; Bossuyt et al. 2002). Species characteristic of thermophilous oak forest are preserved even in the seed banks where above-ground vegetation has been exposed to shade for many years.

The evaluation of seed bank persistence based on a mean value and distribution of LI seems to be more promising in the future than at this moment. Firstly, the list of species to which the authors classified individual species to the 1st, 2nd or 3rd type of seed bank is incomplete. Secondly, the number of records for a species is highly variable, which affects the reliability of calculated LI. However, data obtained in this study allow for the conclusion that the correlation between the duration and intensity of shading of the forest floor and the share of species forming long-term persistent seed banks in disturbed patches of thermophilous oak wood is highly probable.

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