VARIABILITY OF THE SOIL SEED BANKS IN THE NATURAL DECIDUOUS FOREST IN THE BIAŁOWIEŻA NATIONAL PARK

MAŁGORZATA JANKOWSKA-BŁASZCZUK

Department of Botany, Biology Institute,
Higher Pedagogical School,
Konopnicka St.15, 25-406 Kielce
e-mail: mjanko@pu.kielce.pl

(Received: June 24, 1998. Accepted: September 30, 1998)

ABSTRACT

Using the germination method, the species diversity, density of the soil seed bank and its relation to cover vegetation in a natural deciduous forest with primary and secondary tree stand were compared. It was found that the mean density and species composition of the soil seed bank in the forest with secondary tree stand that has spontaneously been overgrown over the last 90 years after clear-cutting does not differ from the soil seed bank derived from primeval forest (3167m^{-2} vs. 3827m^{-2}). In both stands there were 46 species altogether and 36 were common and seed banks were dominated by herbs. The most abundant in this group were: *Urtica dioica*, *Chrysosplenium alternifolium*, *Geranium robertianum*, *Oxalis acetosella*. In both cases it was found that the species structure of the herb layer was similar to that of the seed bank in about 70%. The seed banks of species absent from the herb layer or present there only sporadically were much more abundant. The seedlings of these species constituted more than one third of all seedlings that emerged in the samples from the secondary tree stand and only 5% those from the primary one. The analysis of seed bank in heavily rooted places under primary and secondary tree stands showed that in places with a totally destroyed herb layer the density of the soil seed bank in primeval forest was three times lower than in places with fully developed herb layer structure (102.60 ± 22.61 vs. 307.0 ± 206.5 per sample). This difference under secondary tree stand turned out to be much lower (415.8 ± 137.8 vs. 358.2 ± 126.0 per sample).

KEY WORDS: soil seed bank, disturbance, herb layer, deciduous forest, primeval forest.

INTRODUCTION

The soil seed banks in natural temperate deciduous forests have been the subject of several ecological studies. The changes in its composition during secondary succession from old-fields have been documented by Oosting and Humphreys (1940), Donelan and Thompson (1980), Nakagoshi (1984, 1985), Vankat and Carson (1991). The seed banks in natural communities of temperate deciduous forests are generally considered to be small, poor in species and not reflective of the species composition of the overlying vegetation. Species present in greatest quantity in such banks are generally shade-intolerant and their germination is triggered by micro-climatic changes associated with canopy gaps (Thompson 1992). There is a continuum from species almost never found in the seed bank through those with seed lasting one or only a few years to those lasting at least several decades (Marquis 1975, Canham and Marks 1985). Thompson et al. (1997) have recognised three seed bank types. The classification into transient, short-term persistent and long-term persistent seed banks is based on the comparison of the species in the seed bank and vegetation cover as well as the species frequency in the soil layers subdivided by depth.

There have been very few published studies on the seed banks in natural, undisturbed forest communities, especially

in primeval temperate deciduous forests. The research on the seed bank of hornbeam forest in the Białowieża National Park (Pirożnikow 1983, Jankowska-Błaszczuk and Grubb 1997, Jankowska-Błaszczuk et al. 1998) showed that species of the herb layer, which very often occurred in the seed bank were not always those with high light requirements.

The aim of this work was to show the species diversity and size of the seed bank in a natural deciduous forest depending on the disturbance type. The seed bank was compared between:

- 90-years-old clear-cuts that have been spontaneously overgrown with secondary tree stand and in the surrounding primary forest,
- the patches heavily rooted by wild boars and those with undisturbed multi-layered herb layer both in primary and secondary tree stands.

The following hypotheses were verified:

H₀' In undisturbed patches of the natural hornbeam forest the seed bank is small, species-poor and dominated by the herbs present on the forest floor,

H₀'' There is no difference between the size and species diversity of the seed bank in the primary hornbeam forest and patches where the regeneration process after clear-cutting began about 90 years ago,

H_0 ''' In the patches heavily rooted by wild boars both under the primary and secondary tree stand the size and species diversity of the seed bank are smaller in the places completely covered by herb layer.

MATERIAL AND METHODS

Study sites

The primeval forest, assigned to the *Tilio-Carpinetum*, occupies a large part of the Białowieża National Park (Faliński 1986), and is located in the north-eastern part of Poland (23°31'–24°21'E, 52°29'–52°57'N). The study area, within compartment 316, was characterised in detail by Faliński et al. (1988). There are three parallel belts with secondary tree stand derived from clear-cutting, each 1076 m (1 verst) x 108 m; they alternate with, and are enclosed by, primary forest. In the investigated patch the tree stand is diversified in terms of species composition as well as age and size of trees. The primary forest is dominated by *Carpinus betulus*, *Tilia cordata* and *Quercus robur* which form the lower layer of canopy and cover 80–90% of the area. The highest canopy layer is formed by *Picea abies*. Because of the dense canopy, a mosaic of light conditions on the forest floor varies only from full shade to semi-darkness. During the summer when the foliage is fully developed, no more than 10% of the sunlight penetrates to the ground (Słomka 1967). The forest with secondary tree stand is dominated by *Betula pendula* and *Populus tremula* with some *Picea abies* (the highest tree layer) and remnants of *Salix caprea*, all of which invaded spontaneously. In both forest types there is virtually no shrub layer, and moss layer is very sparse. The herb layer is species-rich and its composition is similar in both cases, but under the secondary tree stand the herb cover is very patchy, with many more bare areas. On average there are 30–40 herbaceous species per 100 m².

Field and laboratory methods

The study compared the easternmost stripe of forest with secondary tree stands described by Faliński et al. (1988) and the strips of primary forest immediately east and west of it; the samples were taken from the northern of two transects crossing the stripes. The shorter transects that consisted of 5 plots were situated under the primary and secondary tree stands in the place where herb layer was totally destroyed by wild boars a year before sampling. The rest of plots were situated in the place with undisturbed herb layer. From the centre of each 2x2 m square one soil monolith 31x31cm (961 cm² area), and 5 cm deep, was collected March 20, 1993, put in a plastic tray, and taken to an unheated glasshouse in the experimental garden of Warsaw University Geobotanical Station in Białowieża. From each sample all underground stems and roots were removed. The soil was thoroughly mixed to promote germination of buried seeds. The trays were unshaded and watered every day from spring to autumn.

Observations were conducted at 10-day intervals during the growing season for four years, from April 10, 1993 to October 30, 1996. On each occasion the numbers of seedlings that could be identified were recorded by species, and then the seedlings were removed, those not immediately identifiable were marked and retained. Identification was based on the previous experience in the forest, a herbarium of seedlings and the atlas of Čsapody (1968). Nomenclature follows Tutin et al. (1980).

In order to relate the species structure of the soil seed bank to the current composition of the herb layer, the species of

herbs and seedlings as well as root suckers of trees up to 50 cm tall in each of the 2x2 squares were recorded three times in 1993. The presence of flowering individuals in each square was recorded on each occasion. For each square the cover of particular species was estimated using the intervals: + < 5%, 1–10%, 2–20%, 3–30%, 4–40% and species without generative shoots were marked in table with (*).

Statistical analysis

The test of Fisher-Snedecor for equality of variance of the seedling's number distribution was conducted for the samples taken under the primary and secondary tree stand. The critical value equals: 1.98 (df: m-1, n-1, m=n=25, α = 0.05).

The statistics F for comparison of variance of the seed bank density between the forests with primary and secondary tree stands equals 1.3752 and is lower than the critical value, thus the hypothesis about equality of variance can be accepted. For comparison of mean density of the seed bank in the samples taken in both forests types the Student's test t was used. With the assumption that the hypothesis H_0 about equality of variance is true the critical value of the test equals 2.011 (df: m+n-2=48, α = 0.05). The statistics t amounts 1.0974 and is lower than the critical value, which means lack of significant differences between the means compared.

Similarity between the species composition of the seed bank and the herb layer was measured by means of the similarity coefficient P of Jaccard-Steinhaus (taking into account qualitative traits – species presence). In the formula $P=2c/a+b$ it was accepted that c was the number of species common to the seed bank and the herb layer, a – the number of species in the seed bank and b – the number of species in the herb layer.

The diversity of the seed banks in each forest stand was calculated using the diversity coefficient of Shannon $H' = -\sum \ln p_i$, where $p_i = n_i/n$; n_i – seedlings number of an i-species, n – sum of seedlings in a particular community.

RESULTS

COMPARISON OF SOIL SEED BANKS DERIVED UNDER PRIMARY AND SECONDARY TREE STANDS IN NATURAL DECIDUOUS FOREST

Size and diversity of species structure

In 25 soil samples taken under the primary tree stand 7610 seedlings (3167/m²) and 40 species were recorded during the four-year observation, whereas in the samples from the secondary tree stand there were 9195 (3827/m²) seedlings of 42 species. In both stands there were 46 species altogether, and 36 were common. Of all seedlings 319 grasses and 4 of dicots were not identified by species.

The mean number of seedlings per a sample amounted to 304.4±220.2 for the samples taken under the primary stand and 367±187.8 for those taken under the secondary one (Fig. 1). The mean number of species was 15±3.4 in the seed bank of the primary tree stand and 17.2±3.5 in that of the secondary one (Fig. 2).

On the grounds of the distribution of the seedlings number in the samples from both forest types (Fig. 1), the hypothesis was formed about equality of the variance of the seed bank size and lack of significant differences between the seed bank densities. The results of the test of Fisher-Snedecor and t-Student confirmed the hypothesis about equality of variance and lack of significant differences between densities of the seed banks studied.

Fig. 1. Number of samples (31x31x5 cm) with a different number of seedlings emerging from seed bank; n=25 for primary tree stand; n=25 for secondary tree stand.

Fig. 2. Number of samples (31x31x5 cm) with a different number of seedlings species emerging from seed bank; n=25 for primary tree stand; n=25 for secondary tree stand.

The diversity of seed banks in each forest stand turned out to be very similar, coefficient of Shanon amounted respectively 2.2141 for primary tree stand and 2.2493 for secondary one.

Perennials

In both forest types – with the primary and secondary tree stand the seed banks were dominated by perennials (Table 1, Fig. 3). The most abundant in this group were: *Urtica dioica*, *Chrysosplenium alternifolium*, *Geranium robertianum*, *Oxalis acetosella*. Some species including *Juncus effusus*, *Carex sylvatica*, *Hypericum perforatum*, *Trifolium repens*, *Scrophularia nodosa*, *Epilobium montanum*, *Veronica serpyllifolia*, *Ajuga reptans* appeared with visibly higher density in the seed bank samples from secondary tree stand, of which the last two were found only in the samples from this forest types.

Annuals and biennials

In both soil seed banks almost the same number of species was found. Totally 9 species were noted, and only *Capsella bursa pastoris* appeared sporadically in the sample from the secondary tree stand. In both cases the most abundant were: *Impatiens noli-tangere* and *Cardamine flexuosa*. As can be seen in Table 1, *Lapsana communis* and *Moehringia trinervia* were several times more numerous in the bank from the primary tree stand.

Shrubs and trees

Altogether in the primary and secondary tree stands there were found 4 species of trees: *Betula pendula*, *Carpinus betulus*, *Picea abies*, *Tilia cordata* and two species of shrubs: *Rubus ideaus*, *Cornus sanguinea*. In both forest stands the most abundant species was *Betula pendula* which made up about 90% of the seed bank in the primary tree stand and 99% in the secondary. The biggest difference was noted for *Carpinus betulus* whose seedlings were present in more than half the samples from the primary tree stand and were completely absent from the seed bank under the secondary one. The seedlings of *Rubus ideaus* were much more frequent and numerous in the samples from the secondary tree stand.

SEED BANKS AND VEGETATION COVER

The floristic composition of the forest floor and species structure of the seed bank in the patches with the primary and secondary tree stand were compared. It was found that in both cases the species structure of the herb layer was similar to that of the seed bank in 68% for primary and 67% for secondary tree stand. In both types of the tree stands the number of species common to the forest floor and seed bank and of the species that appeared exclusively in the seed bank or vegetation cover was very similar (Table 2, Fig. 4).

Generally, the following relationships between the species frequency of the herb layer and seed bank was found:

TABLE 1. Total numbers of seedlings of various species emerging in four successive growing seasons from 50 soil samples (n = 2 x 25 x 0.1 m²) taken from primary and secondary tree stands in natural deciduous forest

	Species	Primary tree stand			Secondary tree stand		
		Σ	Mean number per sample + SE	Mean number/m ²	Σ	Mean number per sample + SE	Mean number/m ²
	Perennials						
1	<i>Urtica dioica</i>	2571	102.84±167.43	1070.05	1445	57.80± 74.65	601.41
2	<i>Chrysosplenium alternifolium</i>	1183	47.32± 44.70	492.36	1549	61.96± 79.26	644.69
3	<i>Juncus effusus</i>	340	13.60± 26.09	141.51	2824	112.96±117.51	1175.35
4	<i>Geranium robertianum</i>	237	9.48± 11.84	98.64	230	9.20± 10.16	95.73
5	<i>Oxalis acetosella</i>	173	6.92± 6.24	72.00	111	4.44± 4.26	46.20
6	<i>Ranunculus lanuginosus</i>	42	1.68± 3.86	17.48	8	0.32± 0.80	3.33
7	<i>Ranunculus repens</i>	34	1.36± 3.50	14.15	54	2.16± 7.73	22.47
8	<i>Geum urbanum</i>	31	1.24± 3.05	12.90	11	0.44± 1.64	4.58
9	<i>Anemone nemorosa</i>	23	0.92± 1.66	9.57	9	0.36± 0.75	3.75
10	<i>Stachys silvatica</i>	22	0.88± 2.88	9.16	16	0.64± 1.32	6.66
11	<i>Glechoma hirsuta</i>	16	0.64± 1.08	6.66	35	1.40± 2.42	14.57
12	<i>Stellaria nemorum</i>	16	0.64± 0.86	6.66	14	0.56± 1.64	5.83
13	<i>Rumex sanguineus</i>	14	0.56± 0.87	5.83	27	1.08± 3.58	11.24
14	<i>Carex sylvatica</i>	9	0.36± 0.57	3.75	208	8.32± 11.80	86.57
15	<i>Hypericum perforatum</i>	8	0.32± 1.07	3.33	152	6.08± 11.06	63.26
16	<i>Lamium galeobdolon</i>	7	0.28± 0.84	2.91	2	0.08± 0.28	0.83
17	<i>Taraxacum officinale</i>	6	0.24± 0.83	2.50	6	0.24± 0.66	2.50
18	<i>Trifolium repens</i>	6	0.24± 0.52	2.50	144	5.76± 6.60	59.93
19	<i>Circaea lutetiana</i>	5	0.20± 0.50	2.08	62	2.48± 8.75	25.80
20	<i>Mentha arvensis</i>	5	0.20± 1.00	2.08	0	0.00± 0.00	0.00
21	<i>Scrophularia nodosa</i>	4	0.16± 0.37	1.66	99	3.96± 14.36	41.20
22	<i>Aegopodium podagraria</i>	3	0.12± 0.44	1.25	0	0.00± 0.00	0.00
23	<i>Cardamine amara</i>	2	0.08± 0.28	0.83	4	0.16± 0.62	1.66
24	<i>Cirsium arvense</i>	2	0.08± 0.28	0.83	3	0.12± 0.33	1.25
25	<i>Epilobium montanum</i>	2	0.08± 0.28	0.83	29	1.16± 3.09	12.07
26	<i>Mycelis muralis</i>	2	0.08± 0.40	0.83	1	0.04± 0.20	0.42
27	<i>Ajuga reptans</i>	0	0.00± 0.00	0.00	29	1.16± 1.68	12.07
28	<i>Asarum europaeum</i>	0	0.00± 0.00	0.00	1	0.04± 0.20	0.42
29	<i>Lathyrus vernus</i>	0	0.00± 0.00	0.00	2	0.08± 0.28	0.83
30	<i>Veronica serpyllifolia</i>	0	0.00± 0.00	0.00	9	0.36± 0.96	3.75
31	<i>Viola reichenbachiana</i>	0	0.00± 0.00	0.00	2	0.08± 0.28	0.83
	Annual and biennial plants						
32	<i>Impatiens noli-tangere</i>	1083	43.32± 52.19	450.74	779	31.16± 26.32	324.22
33	<i>Cardamine flexuosa</i>	660	26.40± 40.61	274.69	837	33.48± 38.77	348.36
34	<i>Lapsana communis</i>	288	11.52± 50.17	119.87	29	1.16± 3.94	12.07
35	<i>Moehringia trinervia</i>	262	10.48± 20.86	109.04	59	2.36± 3.33	24.56
36	<i>Galeopsis tetrahit</i>	32	1.28± 2.03	13.32	28	1.12± 3.19	11.65
37	<i>Stellaria media</i>	20	0.80± 2.27	8.32	4	0.16± 0.47	1.66
38	<i>Polygonum hydropiper</i>	3	0.12± 0.44	1.25	6	0.24± 0.66	2.50
39	<i>Gnaphalium uliginosum</i>	1	0.04± 0.20	0.42	2	0.08± 0.28	0.83
40	<i>Capsella bursa-pastoris</i>	0	0.00± 0.00	0.00	1	0.04± 0.20	0.42
	Shrubs						
41	<i>Rubus idaeus</i>	21	0.84± 1.89	8.74	101	4.04± 3.81	42.04
42	<i>Cornus sanguinea</i>	3	0.12± 0.44	1.25	4	0.16± 0.37	1.66
	Trees						
43	<i>Betula pendula</i>	192	7.68± 5.01	79.91	197	8.00± 5.72	1.97
44	<i>Carpinus betulus</i>	14	0.56± 0.65	5.83	0	0.00± 0.00	0.00
45	<i>Picea abies</i>	4	0.16± 0.37	1.66	1	0.04± 0.20	0.42
46	<i>Tilia cordata</i>	2	0.08± 0.28	0.83	0	0.00± 0.00	0.00
47	Gramineae	260	10.40± 15.6	108.21	59	2.36± 2.68	24.56
48	Unknown	2	0.08± 0.40	0.83	2	0.08± 0.28	0.83

Fig. 3. Percentage of different biological groups of species in the soil seed banks of deciduous forest with primary (P) and secondary (S) tree stands.

Fig. 4. Percentage of number of species occurring in soil seed bank and herb layer of deciduous forest with primary and secondary tree stands.

- the species frequent and abundant in the herb layer were not found at all in the soil samples from both forest types or they appeared there only with a very small number of seeds. These were: *Lamium galeobdolon*, *Ranunculus ficaria*, *Stellaria nemorum*, *Glechoma hirsuta*, *Aegopodium podagraria*, *Stellaria holostea* (Tables 1, 2),
- there is a group of species, such as: *Urtica dioica*, *Oxalis acetosella*, *Chrysosplenium alternifolium*, *Geranium robertianum* with high frequency (over 50%) in the study plots and at the same time with high density in the seed bank both under the primary and secondary tree stand (Tables 1, 2),
- the seed banks formed by the species absent from the herb layer or present there only sporadically are much more abundant in the forest with secondary tree stand. This group includes: *Juncus effusus*, *Carex sylvatica*, *Hypericum perforatum*, *Trifolium repens*, *Epilobium montanum*, *Ajuga reptans*, *Veronica serpyllifolia*, *Scrophularia nodosa*. The seedlings of these species constituted more than one third of all seedlings that emerged in the samples from the secondary tree stand and only 5% those from the primary one (Table 3, Fig. 5).

The seedlings of annuals recorded in the samples from the primary and secondary tree stands belonged in 99% to the species present in the herb layer of both stands. The species with high frequency in the herb layer, such as: *Impatiens noli-tangere*, *Moehringia trinervia*, *Cardamine flexuosa*, *Lapsana communis* were abundant in both seed banks (Table 2).

In the herb layer of the forest with primary tree stand 8 tree species were recorded on the surface of 100 m²: *Carpinus betulus**, *Tilia cordata**, *Acer platanoides*, *Picea abies**, *Ulmus levis*, *Fraxinus excelsior*, *Betula pendula**, *Populus tremula*. Only four of them (marked with an asterisk) were present in the seed bank under the primary stand. In the forest with secondary tree stand the individuals of *Ulmus* and *Fraxinus* were not found in the herb layer, but other tree species were present there. In the seed bank only two species emerged: *Betula pendula* and *Picea abies*. In both cases the seed banks of trees were dominated by the seedlings of *Betula*, which constitute more than 95%. In the seed bank of trees under the primary tree stand *Carpinus betulus* was much more frequent and there were more species in comparison with the seed bank under the secondary tree stand.

In the study plots only one shrub species *Rubus ideaus* was noted, and in the forest with secondary tree stand this shrub (mainly its seedlings and juvenile individuals) was twice more frequent. In the seed bank of this forest *Rubus* was five times more abundant. In both seed banks some seedlings of *Cornus sanguinea* were recorded. This species was not found in the herb layer.

SEED BANKS IN DISTURBED AND UNDISTURBED PLACES

Primary tree stand

It was found that density of the seed bank in heavily rooted places is three times lower than in places with undisturbed herb

TABLE 2. Comparison of frequency of seedlings of species in the herb layer and soil seed bank of lindenhornbeam forest with primary and secondary tree stands. Frequency of species on herb layer estimated basing on data from $2 \times 25 \times 4 \text{ m}^2$ plots, and frequency in seed bank was estimated basing on presence of seedlings emerging in samples $n = 2 \times 25 \times 0.1 \text{ m}^2$ taken from the plots where species of herb layer were recorded; * – not identified

	Species	Primary tree stand		Secondary tree stand	
		Herb layer	Seed bank	Herb layer	Seed bank
		Frequency %		Frequency %	
	Perennials				
1	<i>Lamium galeobdolon</i>	96	16	68	8
2	<i>Ranunculus ficaria</i>	92	0	92	0
3	<i>Oxalis acetosella</i>	92	96	88	96
4	<i>Stellaria nemorum</i>	88	44	84	24
5	<i>Anemone nemorosa</i>	80	40	72	24
6	<i>Glechoma hirsuta</i>	76	32	88	52
7	<i>Urtica dioica</i>	76	96	72	96
8	<i>Chrysosplenium alternifolium</i>	72	96	68	88
9	<i>Geranium robertianum</i>	68	84	40	88
10	<i>Ranunculus lanuginosus</i>	64	28	60	16
11	<i>Aegopodium podagraria</i>	40	8	32	0
12	<i>Geum urbanum</i>	36	32	28	12
13	<i>Stachys silvatica</i>	32	20	28	28
14	<i>Stellaria holostea</i>	20	0	28	0
15	<i>Circaea lutetiana</i>	16	16	8	16
16	<i>Rumex sanguineus</i>	16	36	12	32
17	<i>Cardamine amara</i>	12	8	0	8
18	<i>Poa nemoralis</i>	12	*	28	*
19	<i>Dentaria bulbifera</i>	8	0	4	0
20	<i>Viola reichenbachiana</i>	8	0	8	8
21	<i>Carex remota</i>	8	0	12	0
22	<i>Mycelis muralis</i>	8	4	4	4
23	<i>Asperula odorata</i>	8	0	14	0
24	<i>Ranunculus repens</i>	8	28	12	20
25	<i>Rumex obtusifolius</i>	8	0	4	0
26	<i>Milium effusum</i>	8	*	4	*
27	<i>Festuca gigantea</i>	8	*	0	*
28	<i>Lathyrus vernus</i>	4	0	0	8
29	<i>Scrophularia nodosa</i>	4	16	8	36
30	<i>Lathraea squamaria</i>	4	0	0	0
31	<i>Carex sylvatica</i>	4	32	4	80
32	<i>Isopyrum thalictroides</i>	4	0	0	0
33	<i>Anemone ranunculoides</i>	4	0	4	0
34	<i>Ajuga reptans</i>	0	0	8	48
35	<i>Asarum europaeum</i>	0	0	4	4
	Annual and biennial plants				
1	<i>Impatiens noli-tangere</i>	72	76	76	88
2	<i>Moechringia trinervia</i>	64	76	80	60
3	<i>Cardamine flexuosa</i>	48	76	58	88
4	<i>Lapsana communis</i>	36	44	12	16
5	<i>Galeopsis tetrahit</i>	16	44	12	40
6	<i>Stellaria media</i>	8	24	16	12
	Shrubs and trees				
1	<i>Carpinus betulus</i>	76	52	58	0
2	<i>Tilia cordata</i>	32	8	24	0
3	<i>Acer platanoides</i>	20	0	16	0
4	<i>Rubus idaeus</i>	16	32	28	76
5	<i>Picea abies</i>	12	16	8	4
6	<i>Ulmus glabra</i>	8	0	0	0
7	<i>Fraxinus excelsior</i>	4	0	0	0
8	<i>Betula pendula</i>	4	96	12	100
9	<i>Populus tremula</i>	4	0	16	0

TABLE 3. Frequency of seedlings of species which were sparse or absent from the herb layer and emerged from soil seed bank in samples (n=2x25x0.1 m²) taken from forest with primary and secondary tree stands

Species	Primary tree stand		Secondary tree stand	
	Frequency %	Mean number/m ²	Frequency %	Mean number/m ²
Perennials				
1 <i>Juncus effusus</i>	84	141.5	96	1175.4
2 <i>Hypericum perforatum</i>	12	3.3	60	63.3
3 <i>Taraxacum officinale</i>	12	2.5	16	2.5
4 <i>Cirsium arvense</i>	4	0.8	12	0.1
5 <i>Epilobium montanum</i>	8	0.8	20	12.1
6 <i>Trifolium repens</i>	20	2.5	92	59.9
7 <i>Veronica serpyllifolia</i>	0	0.0	16	3.8
8 <i>Mentha arvensis</i>	4	2.1	0	0.0
Annual and biennial plants				
1 <i>Polygonum hydropiper</i>	8	1.3	16	2.5
2 <i>Gnaphalium uliginosum</i>	4	0.4	8	0.8
3 <i>Capsella bursa-pastoris</i>	0	0.0	4	0.4
Shrubs and trees				
1 <i>Cornus sanguinea</i>	8	1.3	16	1.7

Fig. 5. Number of seedlings emerging from soil seed banks of deciduous forest with primary (P) and secondary (S) tree stands, species which were absent or sparse in the herb layer.

layer (102.6±22.6 vs. 307.0±206.5 per sample). However, the species composition of both seed banks is similar (the coefficient of J-S over 75%, Table 4). The seed bank in places disturbed by wild boars is characterised by a higher density of only two species: *Juncus effusus* and *Betula pendula*. At the same time species frequent in the herb layer, such as: *Cardamine flexuosa*, *Chrysosplenium alternifolium*, *Geranium robertianum*, *Impatiens noli-tangere*, *Lapsana communis*, *Urtica dioica* were much less abundant in the seed bank there.

Juncus effusus and *Betula pendula* constituted about 60% of the total number of seedlings.

Secondary tree stand

The differences between seed bank density in the destroyed and undestroyed places turned out to be much lower in the forest with secondary than in that with primary tree stand (415.8±137.8 vs. 358.2±126.0 per sample). In the forest with secondary tree stand in places disturbed by animals *Juncus*

TABLE 4. Cover of species in the herb layer (on 2x20 m² plots) and number of seedlings emerged from seed banks (2x5x0.1 m² samples) taken from the same plots situated in undisturbed and disturbed patches in forest with primary and secondary tree stand. (cover of vegetation + %, 1-10%, 2-20%, 3-30%), * – no generative shoots

Species	Primary tree stand				Secondary tree stand			
	Seedlings from seed bank		Herb layer		Seedlings from seed bank		Herb layer	
	Disturbed	Undisturbed	Disturbed	Undisturbed	Disturbed	Undisturbed	Disturbed	Undisturbed
<i>Acer platanoides</i>	0	0	0	0	0	0	+	+
<i>Aegopodium podagraria</i>	0	2	0	+	0	0	0	+
<i>Ajuga reptans</i>	0	0	0	0	7	5	0	0
<i>Anemone nemorosa</i>	1	10	+	+	1	2	+	+
<i>Asarum europaeum</i>	0	0	0	0	0	1	0	+
<i>Asperula odorata</i>	0	0	0	0	0	0	0	+
<i>Betula pendula</i>	46	19	0	0	57	27	+	0
<i>Capsella bursa-pastoris</i>	0	0	0	0	0	0	0	0
<i>Cardamine amara</i>	0	0	0	0	4	0	0	0
<i>Cardamine flexuosa</i>	33	60	+	+	39	210	0	+
<i>Carex sylvatica</i>	5	2	0	0	73	27	0	+
<i>Carpinus betulus</i>	5	2	+	+	0	0	+	+
<i>Chrysosplenium alternifolium</i>	46	112	+	+	4	334	+	+
<i>Circaea lutetiana</i>	2	1	0	+	0	53	+	+
<i>Cirsium arvense</i>	1	0	0	0	0	1	0	0
<i>Cornus sanguinea</i>	2	0	0	0	1	1	0	0
<i>Dentaria bulbifera</i>	0	0	0	0	0	0	0	+
<i>Epilobium montanum</i>	1	1	0	0	0	0	0	0
<i>Galeobdolon luteum</i>	0	4	+	1	0	0	+	1
<i>Galeopsis tetrahit</i>	1	14	0	+	1	2	+	+
<i>Geranium robertianum</i>	1	75	0	1	6	47	+	1
<i>Geum urbanum</i>	0	16	0	0	0	8	0	+
<i>Glechoma hederacea</i>	0	6	0	1	4	7	+	+
<i>Gnaphalium uliginosum</i>	0	0	0	0	0	0	0	0
<i>Hypericum perforatum</i>	2	0	0	0	0	35	0	0
<i>Impatiens noli-tangere</i>	1	126	+	1	34	159	+	1
<i>Juncus effusus</i>	257	7	0	0	1381	309	0	0
<i>Lapsana communis</i>	0	272	+	1	0	28	0	1
<i>Lathyrus vernus</i>	0	0	0	0	2	0	0	+
<i>Mentha silvatica</i>	5	0	0	0	0	0	0	0
<i>Moehringia trinervia</i>	16	136	+	+	9	19	+	+
<i>Mycelis muralis</i>	0	0	0	0	1	0	0	0
<i>Oxalis acetosella</i>	19	25	+	+	8	27	+	1
<i>Picea abies</i>	0	2	0	0	0	0	0	0
<i>Polygonum hydropiper</i>	0	0	0	0	1	4	0	0
<i>Populus tremula</i>	0	0	0	0	0	0	0	+
<i>Ranunculus lanuginosus</i>	0	21	+	+	0	2	+	1
<i>Ranunculus repens</i>	1	26	0	0	0	0	0	0
<i>Rubus ideaus</i>	9	7	+	+	21	18	+	+
<i>Rumex sanguineus</i>	4	5	0	0	1	21	0	+
<i>Scrophularia nodosa</i>	1	2	0	0	0	88	0	+
<i>Stachys sylvatica</i>	1	15	0	1	0	6	+	+
<i>Stellaria holostea</i>	0	0	0	0	0	0	0	+
<i>Stellaria media</i>	2	0	0	0	0	2	0	0
<i>Stellaria nemorum</i>	0	4	0	3	1	1	0	2
<i>Taraxacum officinale</i>	1	1	0	0	0	0	0	0
<i>Tilia cordata</i>	0	1	+	+	0	0	+	0
<i>Trifolium repens</i>	1	3	0	0	52	33	0	0
<i>Urtica dioica</i>	41	424	+	2	69	572	+	2
<i>Veronica serpyllifolia</i>	0	0	0	0	0	6	0	0
<i>Viola reichenbachiana</i>	0	0	0	0	2	0	+	+

constitutes as much as 94% of the whole seed bank and its mean density is much higher than in the forest with primary tree stand. In the forest with secondary tree stand some species were more abundant in the seed bank in rooted places than in undisturbed ones. There were: *Trifolium repens*, *Rubus idaeus*, *Juncus effusus*, *Carex sylvatica*, *Betula pendula*.

DISCUSSION

General nature of seed bank in the temperate deciduous forest

One of the affirmed regularities concerning seed banks in temperate deciduous forests is the fact that their size and species diversity do not depend on the diversity of the herb, shrub or tree layers, but on the degree to which a forest community remains primeval as well as frequency and quality of disturbances occurring there. Many ecological studies concerning the changes of seed banks during successional series show that the richest and most abundant storage of seeds in soil can be found in early succession community, therefore in undisturbed or old growth forest seed numbers are generally low (Oosting and Humphreys 1940, Livingston and Allesio 1968, Pickett, McDonnell 1989, Kellman 1970, 1974, Johnson 1975, Strickler and Edgerton 1976, Whipple 1978, Pirożnikow 1983, Petrov and Palkina 1983, Conn, Cochrane and Delapp 1984, Petrov 1987, Staaf et al. 1987).

The results of four-year observations of the seedlings emergence in the samples taken from the Białowieża hornbeam forest did not confirm the hypothesis about the low density and species poverty of the seed bank. In comparison with other data concerning the size of the seed bank in temperate

deciduous forests (Table 5) the seed bank in this study is relatively large, especially if we take into consideration the fact that the community is still quite natural. The data presented in this work differ ten times from those obtained by Pirożnikow (1983) for the seed bank of the same forest community. Perhaps the key difference between the studies was that in my studies the soil surface was much disturbed by the removal of roots and rhizomes, and by stirring at intervals, while her account of methods does not mention any disturbance of the soil. However, if we compare the results given in this study with those for early successional communities forming old meadows or fields for a dozen or tens of years, it seems obvious that such communities are characterised by more abundant seed banks (a few thousand or several thousand seeds per m²) (Symonides 1986, Leck and Parker 1989). During the secondary succession in the seed bank of a tens-year-old forest there are still viable propagules of many early successional herbs, that have not been found in the shady forest community for many years. The most persistent components of the seed bank in a tens-years-old deciduous or coniferous forest are seeds of the species that were abundant in the previous stages of succession. The other components of the seed bank are short-lived propagules of the species present in the seed bank with low or high density depending on a species. Among the most persistent components of the seed bank there are highly light-demanding genera, such as: *Juncus* spp., *Calluna* spp., *Hypericum* spp., *Trifolium* spp., *Rubus* spp., *Poa* spp., *Veronica* spp., mentioned in the literature most often (Thompson et al. 1997). Seeds of many species from these genera can remain viable in the soil for several dozen of years. The presence of such species in the Białowieża hornbeam forest (Pirożnikow 1983, Jankowska-Błaszczuk and

TABLE 5. Densities (seeds/m²) of buried seeds in soil seed banks for broadleaved forest

Forest type	Nature of sample	Density (m ⁻²)	Authors
<i>Tilia-Carpinus-Quercus-Picea</i> primeval forest	5 cm deep plus litter	3437	Błaszczuk & Grubb (1997)
Oak forest	10 cm deep without litter	1108	Błaszczuk et al. (1998)
<i>Tilia-Carpinus-Quercus-Picea</i> primeval forest	8 cm deep	190	Pirożnikow (1983)
<i>Carici elongatae-Alnetum</i> primeval forest	10 cm deep	2051	Falińska (1981)
<i>Fagus</i> (>100-yr-old managed stands)	5 cm deep plus litter	1391-2514	Staaf et al. (1987)
<i>Fagus-Betula-Acer</i> primary forest	5 cm deep plus litter	1806	Graber & Thompson (1978)
<i>Fagus</i> (mix of primary and old secondary)	10 cm deep including litter	218-485	Nakagoshi (1984)
<i>Quercus-Carya</i>	13.5 cm deep	1181	Oosting & Humphreys (1940)
<i>Betula-Acer</i> (90 years old)	10 cm deep	3400	Moore & Wein (1977)
<i>Acer-Fagus</i> (90 years old)		1950	
<i>Quercus-Tilia</i> (90 years old)	10 cm deep	6500	Petrov & Palkina (1983)
Oak forest	10 cm deep	1100	Petrov (1987)

Grubb 1997, Jankowska-Błaszczuk et al. 1998) indicates that their seeds are dispersed at a long distance and can be viable in the soil for prolonged periods.

From most studies concerning seed banks of temperate deciduous forests one can conclude that trees do not produce long-lived seeds (Clark and Boyce 1964, Hayashi and Numata 1964, Howard and Ashton 1967, Frank and Safford 1970, Marquis 1975, Fraser 1976, Payette et al. 1982, Conn et al. 1984, Staff et al. 1987 after Thompson 1992, Warr et al. 1994). My results unambiguously confirm the hypothesis that the seed banks in deciduous forest are dominated by perennials. Of the eight tree species in the seed bank of the hornbeam forest only the early successional and highly light-demanding *Betula pendula* was very frequent. According to Thompson (1992) natural selection did not favour the accumulation of a persistent seed bank in the long-lived dominants of late successional, stable and relatively undisturbed ecosystems.

Marks (1983) suggests that in climax forest communities in absence of human disturbance there is a group of plants specialized in setting in nearly formed gaps in the tree canopy. Among such plants there are trees and shrubs (for instance *Prunus pensylvanica* and *Rubus strigosus*), of which the seeds are long-lasting and well adapted to the dispersal at a long distance.

The comparison of the species composition of the seed bank and herb layer led me to conclude that the seed bank is mostly formed by the herb layer species. The species occurring with high frequency in the seed bank of the shady hornbeam forest are at the same time typical components of the herb layer, for example: *Urtica dioica*, *Oxalis acetosella* or *Geranium robertianum*. These species were also found in the seed banks of the Białowieża forests by other authors (Pi- rożnikow 1983, Falińska 1996, Jankowska-Błaszczuk and Grubb 1997, Jankowska-Błaszczuk et al. 1998). The seeds of these species can retain viability in the soil for more than four years, which become visible during the observation on the rate of seedlings emergence (Jankowska-Błaszczuk unpublished data). Many authors disagree about how long the seed banks formed by these species can persist in the soil (Thompson et al. 1997). The species that occurred frequently in the herb layer of the hornbeam forest, but were absent from the seed bank or rarely present (*Lamium galeobdolon*, *Ranunculus ficaria*, *Stellaria nemorum*, *Glechoma hirsuta*, *Aegopodium podagraria*) were mainly those producing few or short-lived seeds.

Composition of soil seed bank under primary and secondary tree stands

The results of the study of the seed bank in the patches with primary and secondary 90-year-old tree stands confirmed the hypothesis that the seed banks do not differ in their density and species composition. When the herb layer in both patches is very similar there is only a visible difference in the contribution of species absent from the herb layer. In the patch, where the trees were cut about 90 years ago, in the seed bank there are many more species absent from the herb layer and characterised by high light-demand. The difference in density of seedlings and frequency in the seed bank is clearly marked for *Juncus effusus*, *Hypericum perforatum*, *Trifolium repens*, *Epilobium montanum*. It seems highly probable that these species appeared profusely in the gaps as soon as the trees were cut, and next they began to withdraw from the forest floor as a result of closing of the tree canopy and shading. In the ecological literature many data show that these are ubiquitous long-lived seeds that occur in the seed

banks of entirely different plant communities (Thompson et al. 1997).

Size and diversity of seed bank after small-scale disturbance

In the ecological literature it is often emphasized that the survival strategy based on forming of a persistent seed bank is the effect of the adaptation to disturbance (Grime and Hillier 1992, Thompson 1992). In the case of stable forest communities the notion of disturbance is related by many authors to forming of a gap in the tree canopy and a rapid change of light conditions on the forest floor (Pickett and White 1985). In this study the seed banks in the patches rooted by wild boars and the undisturbed ones were compared (only the upper layer of the soil was deeply dug, and the canopy closure remained unchanged). As was expected, in the forest with primary tree stand in the patches rooted the seed bank turned out to be several times smaller a year after the disturbance. This confirms the hypothesis that the seed bank of the hornbeam forest is mainly formed by the herb layer species, whose seeds are dispersed directly into the soil. The seeds lose viability in the soil after 2-3 years. It is interesting that in the forest with secondary tree stand the difference in the seed bank density between disturbed and undisturbed places is much smaller than that in the forest with primary tree stand. This is due to the fact that also in undisturbed places the contribution of the species absent from the herb layer is eight times bigger under the secondary tree stand than under the primary.

In both cases in places disturbed by animals the contribution of *Juncus effusus* to the seed bank increases from 31% to 94% under the secondary tree stand and from 4% to 50% under primary one.

Functional groups of herbs and shrubs species in the seed bank

Jankowska-Błaszczuk and Grubb (1997) divided the herb and shrub species present in the seed bank of the Białowieża hornbeam forest into two functional groups. The species in group A (*Juncus effusus*, *Trifolium repens*, *Hypericum perforatum*, *Scrophularia nodosa*, *Ajuga reptans*, *Epilobium montanum*) clearly represent a strategy of waiting for large-scale disturbances to the canopy tree, they benefit from large-scale opening of the canopy. This group of species is much more abundant in seed bank from forest with secondary tree stands (Fig. 5). The second group B consists of species which do not need large-scale disturbance of the tree canopy for establishment (*Urtica dioica*, *Chrysosplenium alternifolium*, *Geranium robertianum*, *Oxalis acetosella*, *Stachys sylvatica*, *Stellaria nemorum*, *Galeopsis tetrahit*, *Geum urbanum*, *Impatiens noli-tangere*, *Cardamine flexuosa*, *Lapsana communis*, *Moehringia trinervia*). Group B species benefit from single-treefall gaps in the tree canopy, but appear to be suited primarily to gaps in the canopy of the herb layer and in the root layer made mainly by animals. This study showed that in the places heavily rooted by wild boars in the seed bank there are eight times fewer B species, but their seedlings appear on the surface much more frequent than those of species A. Although species A are abundant in the seed bank, their seedlings are not found in the herb layer under tree canopy.

ACKNOWLEDGEMENTS

I thank Professor Janusz B. Faliński for enabling me to do my research in the permanent plot, as well as in the glass-house of the Białowieża Geobotanical Station, and also Professor Krystyna Falińska for methodological consultations and discussions about seed banks.

LITERATURE CITED

- CANHAM C.D., MARKS P.L., 1985. The response of woody plants to disturbance: patterns of establishment and growth. pp. 197-216 In Pickett S.T.A., White P.S. (Eds.) *The ecology of natural disturbance and patch dynamics*. Orlando, Academic Press.
- CONN J.S., COCHRANE C.L., DELAPP J.A., 1984. Soil seed bank changes after forest clearing and agricultural use in Alaska. *Weed Sci.* 32: 343-347.
- CLARK F.B., BOYCE S.G., 1964. Yellow-poplar seed remain viable in the forest litter. *Journal of Forestry* 62: 564-567.
- CSAPODY V., 1968. *Keimlings Bestimmungsbuch der Dikotyledonen*. Akadémiai Kiadó, Budapest, pp. 286.
- DONELAN M., THOMPSON K., 1980. Distribution of buried viable seeds along a successional series. *Biological Conservation* 17: 297-311.
- FALIŃSKA K., 1996. *Ekologia Roślin*. PWN, Warszawa, pp. 453.
- FALIŃSKI J.B., 1986. Vegetation dynamics in temperate lowland primeval forests. Dordrecht, Junk.
- FALIŃSKI J.B., CANULLO R., BIAŁY K., 1988. Changes in the herb layer, litter fall and soil properties under primary and secondary tree stands in a deciduous forest ecosystem. *Phytocoenosis* 1 (NS): 1-49.
- FRANK R.M., SAFFORD L.O., 1970. Lack of viable seeds in the forest floor after clearcutting. *Journal of Forestry* 68: 776-778.
- FRASER J.W., 1976. Viability of black spruce seed in or on a boreal forest seed bed. *Forestry Chronicle* 52: 229-231.
- GRABER R.E., THOMPSON D.F., 1978. Seeds in the organic layers and soil of four beech-birch-maple stands. Research Paper – USDA Forest Service No. NE-401.
- GRIME J.P., HILLIER S.H., 1992. The contribution of seedling regeneration to the structure and dynamics of plant communities and larger units of landscape. In: M. Fenner (ed.) *The ecology of regeneration in plant communities*. CAB INTERNATIONAL Wallingford.
- HOWARD T.M., ASHTON D.H., 1967. Studies of soil seed in snow gum woodland (*E. pauciflora* Sieb. ex Spreng var. *alpina* (Benth) Ewart). *Victorian Naturalist* 84: 331-335.
- HAYASHI I., NUMATA M., 1964. Ecological studies on the buried-seed population in the soil from the view-point of plant succession. III. A mature stand of *Pinus thunbergii*. *Physiological Ecology* 12: 185-190.
- JANKOWSKA-BŁASZCZUK M., GRUBB P.J., 1997. Soil seed banks in primary and secondary deciduous forest in Białowieża, Poland. *Seed Science Research* 7: 281-292.
- JANKOWSKA-BŁASZCZUK M., KWIATKOWSKA A.J., PANUFNIK D., TANNER E., 1998. The size and diversity of the soil seed banks and the light requirements of the species in sunny and shady natural communities of the Białowieża Primeval Forest. *Plant Ecology* 136: 105-118.
- JOHNSON E.A., 1975. Buried seed populations in the subarctic of Great Slave Lake, Northwest Territories. *Can. J. Bot.* 53: 2933-2941.
- KELLMAN M.C., 1970. The viable seed content of some forest soil in coastal British Columbia. *Can. J. Bot.* 48: 1383-1385.
- KELLMAN M.C., 1974. Preliminary seed budgets for two plant communities in coastal British Columbia. *J. Biogeog.* 1: 123-133.
- KJELLSON G., 1992. Seed banks in Danish deciduous forests: species composition, seed influx and distribution pattern in soil. *Ecography* 15: 86-100.
- LECK M.A., PARKER V.T., SIMPSON R.L., (eds.) 1989. *Ecology of Soil Seed Banks*. Academic Press, Inc. San Diego, California.
- LIVINGSTON R.B., ALLESSIO M., 1968. Buried viable seed in successional field and forest stands, Harvard Forest, Massachusetts. *Bull. Torrey Bot. Club* 95: 58-69.
- MARKS P.L., 1983. On the origin of the field plants of the northeastern United States. *American Naturalist* 122: 210-228.
- MARQUIS D.A., 1975. Seed storage and germination under northern hardwood forest. *Canadian Journal of Forest Research* 5: 478-484.
- MOORE J.M., WEIN R.W., 1977. Viable seed populations by soil depth and potential site recolonization after disturbance. *Canadian Journal of Botany* 55: 2408-2412.
- NAKAGOSHI N., 1984. Buried viable seed populations in forest communities on the Hiba Mountains, south-western Japan. *Journal of Science of the Hiroshima University, Series B, Division 2*, 19: 1-56.
- NAKAGOSHI N., 1985. Buried viable seeds in temperate forests. pp. 551-570 in White J. (Ed.) *The population structure of vegetation*. Dordrecht, Junk.
- OOSTING H.F., HUMPHREYS M.E., 1940. Buried viable seeds in a successional series of old field and forest soils. *Bulletin of the Torrey Botanical Club* 67: 253-273.
- PAYETTE S., DESHAYE J., GILBERT H., 1982. Tree seed populations at the treeline in Rivière aux Feuilles area, northern Quebec, Canada. *Arctic and Alpine Research* 14: 215-222.
- PETROV V.V., 1987. Seed bank in the soil of broad leaved forest. (New data). *Vestnik Moskovskogo Universiteta Biologiya* 42: 55-59.
- PETROV V.V., PALKINA T.A., 1983. Content of dormant viable seeds in the soil of a natural broad leaved forest and a spruce plantation. *Vestnik Moskovskogo Universiteta, Biologiya* 38: 31-35.
- PICKETT S.T.A., WHITE P., 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando.
- PICKETT S.T.A., McDONNELL M.J., 1989. Seed bank dynamics in temperate deciduous forest. In: Leck, M.A., Parker V.T., Simpson R.L. (eds.), *Ecology of Soil Seed Banks*. Academic Press, San Diego, CA, pp. 123-147.
- PIROŽNIKOW E., 1983. Seed bank in the soil of stabilized ecosystem of a deciduous forest (*Tilio-Carpinetum*) in the Białowieża National Park. *Ekol. Pol.* 31: 145-172.
- SŁOMKA J., 1967. Remarks on the bioclimate of the interior of a forest (material from a *Carpinetum typicum* biotope) in the Białowieża National Park. *Ekol. pol.* B 13: 309-323.
- STAARF H., JONSSON M., OLSEN L.G., 1987. Buried germinative seeds in mature beech forests with different herbaceous vegetation and soil types. *Holarctic Ecology* 10: 268-277.
- STRICKLER G.S., EDGERTON P.J., 1976. Emergent seedlings from coniferous litter and soil in Eastern Oregon. *Ecology* 57: 801-807.
- SYMONIDES E., 1986. Seed bank in old-field successional ecosystems. *Ekol. Pol.* 33: 61-80.
- TUTIN T.G., HEYWOOD V.H., BURGESS N. A., MOORE D.M., VALENTINE D.H., WALTERS S.M., WEBB D.A., 1964-80. *Flora Europea*, Vols 1-5. Cambridge, Cambridge University Press.
- THOMPSON K., 1992. The functional ecology of seed banks. pp. 231-257. In Fenner M. (Ed.) *Seeds and ecology of regeneration in plant communities*. Wallingford, CAB INTERNATIONAL
- THOMPSON K., BAKKER J., BEKKER R., 1997. The soil seed banks of North West Europe: methodology, density and longevity. Cambridge University Press. Cambridge, pp. 276.
- VANKAT J.L., CARSON W.P., 1991. Floristics of a chronosequence corresponding to old field deciduous forest succession in southwestern Ohio. II. Post disturbance vegetation. *Bulletin of the Torrey Botanical Club* 118: 385-391.
- WARR S.J., KENT M., THOMPSON K., 1994. Seed bank composition and variability in five woodlands in south-west England. *Journal of Biogeography* 21: 151-168.
- WHIPPLE S.A., 1978. The relationship of buried, germinating seeds to vegetation in an old-growth Colorado subalpine forest. *Can. J. Bot.* 56: 1505-1509.

ZMIENNOŚĆ GLEBOWEGO BANKU NASION W NATURALNYM LESIE LIŚCIASTYM BIAŁOWIESKIEGO PARKU NARODOWEGO

STRESZCZENIE

Porównywano bogactwo gatunkowe, zagęszczenie oraz podobieństwo banku nasion do składu gatunkowego runa w naturalnym lesie grądowym z pierwotnym i wtórnym drzewostanem. Bank nasion oceniano metodą wschodów siewek. Stwierdzono, że skład gatunkowy oraz średnie zagęszczenie banku nasion pochodzącego z płatów lasu podlegającego od 90 lat spontanicznej regeneracji nie różni się istotnie od banku nasion pochodzącego z płatów o drzewostanie pierwotnym (3167m^{-2} vs. 3872m^{-2}). Razem stwierdzono 46 gatunków z czego 36 wystąpiło w obu typach stanowisk a banki nasion zarówno spod pierwotnego, jak i wtórnego drzewostanu zdominowane były przez rośliny zielne. W obu przypadkach stwierdzono, że struktura gatunkowa warstwy runa jest odzwierciedlana w banku nasion w około 70%. Bank nasion gatunków nieobecnych w runie lub występujących tam sporadycznie jest znacznie liczniejszy pod wtórnym drzewostanem. Siewki tych gatunków stanowiły ponad 1/3 wszystkich siewek pojawiających się w próbach z lasu o wtórnym drzewostanie i tylko 5% w próbach z lasu pierwotnego. Analiza banku nasion pochodzącego z miejsc silnie buchtowanych przez dziki wykazała, że w lesie o pierwotnym drzewostanie zagęszczenie spada trzykrotnie w porównaniu z miejscami o niezaburzonym runie, natomiast te różnice w lesie wtórnym okazały się znacznie mniejsze.

SŁOWA KLUCZOWE: glebowy bank nasion, zaburzenie, warstwa runa, las liściasty, las pierwotny.