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SEED BANK IN OLD-FIELD SUCCESSIONAL ECOSYSTEMS

ABSTRACT: The size, species composition and spatial structure of the seed bank in the soil were studied in four uneven-aged old fields, in early Peucedano-Pinetum forest succession phases. In the seed bank of the successional ecosystem series the following phenomena have been found: (1) decrease in the number of seed and species, (2) increased seasonal stability of the numbers and species composition of seeds, (3) presence of all the species occurring in the phytocoenosis, and a similar list of dominants, (4) similar type of seed distribution in the soil. A significant influence has also been found of the vegetation structure on the seed rain to seed bank ratio, as well as a low germination percentage of seeds accumulated in the surface soil layer.

KEY WORDS: Size of seed bank, composition of seed bank, seed rain, old-field succession, spatial structure of seed bank.

1. INTRODUCTION

Studies carried out so far indicate that the number of seeds accumulated in the surface soil layer to some extent characterizes the type of ecosystem; the lower the proportion of therophytes in the vegetation composition, the lower the number of seeds. In agrocenoses in which annuals are dominant the bank contains 38 up to 70 thousand seeds per 1 m² soil (Brenchley and Warrington 1930, 1945), while in psammophilous sods there are from 38 to 48 thousand seeds per the same unit surface area (Symonides 1979), in multispecific meadows with *Geranium pratense* L. about 17 thousand (Rabotnov 1956), in birch brushwoods about 14 thousand (Karpov 1969), in stable forest ecosystems of various types — at the most several thousand per 1 m² soil (Zarzycki 1964, Petrov 1977, Falińska 1981, Pirożnikow 1983).

As indicated by some data, in stable ecological systems the seed bank size can be almost constant (Thompson and Grime 1979); it is subject to great

variation in locally devastated areas, as well as in the course of ecosystem succession (Lippert and Hopkins 1950, Numata et al. 1964, Livingstone and Alessio 1968). Whatever the ecosystem type, the species composition of the seed in the soil is richer than the specific composition of the vegetation that covers it: several times in pioneer ecosystems and only slightly in stabilized forest ecosystems. But whereas at the early successional stages all the species of the phytocoenose are represented in the seed bank, at the final one — there only occurs a certain percentage of species (Rysin and Rysina 1965, Karpov 1969, Symonides 1978, Pirožnikow 1983).

The above-quoted data permit hypotheses to be formulated concerning the directional changes in numbers and specific composition of the seed bank in the ecosystem succession process. For a series leading on to a forest community, as a climax, the following direction of changes can be hypothetically assumed: (1) a fall in the total number of seeds in the bank, (2) a decrease in the total number of species represented by seeds in the soil, (3) a decrease in the number of phytocoenose-present species in the floristic composition of the seed bank, and (4) an increased seasonal stability of the number and specific composition of seeds in the bank.

The main purpose of the studies presented in this paper was to verify the above hypotheses with regard to the early regenerative succession phases of a pine forest, Peucedano-Pinetum Mat. (1962) 1973. Apart from this, it has been tried to answer the question: if and to what extent the seed bank structure and dynamics are correlated with the plant community structure and dynamics in the course of ecosystem succession.

The present study is part of comprehensive research into the course of a spontaneous, secondary succession in old fields. Two earlier publications have been devoted to changes in the floristic composition and species diversity of phytocoenoses, and to changes in the state, species structure and spatial structure of the phytomass over four successive regeneration phases of a forest community (Symonides 1985, Symonides and Borowiecka 1985).

The studies were carried out in the years 1980–1982 in four old fields, at the southwestern edge of the Białowieża Primaeval Forest, within the historical, 16th-century boundaries of the latter. The fields selected for the studies were located in a Peucedano-Pinetum forest habitat. In 1980, they were 6, 10, 16 and 26 years old. They represent — respectively — 3rd, 4th, 5th and 6th succession phases of the eight succession phases distinguished by Faliński (1980) in a whole series lasting about 70 years. A synthetic description of the vegetation and soils of the particular fields can be found in the first paper of the series presented (Symonides 1985).

2. METHODS

The numbers, species composition and distribution of the seeds in the soil of the old fields studied were estimated in 1980 and 1981, twice in each year: in spring (May), and in autumn (September). On account of the phenology of germination and dispersal of

the seeds of most species, it could be assumed that at the first date the seasonal minimum, and at the second — the seasonal maximum seed numbers in the bank would occur.

Soil samples were collected in a grid of 30 shifted squares, 1 m in side-length each (Fig. 1). The centre of a square was at the same time the centre of a circle 0.01 m² in area, within which two-centimetre layers of previously moistened soil were cut out, at depths from 0.5 cm down to 14.5 cm. Air-dry soil was put through sieves of different mesh size. Undamaged seeds were identified and counted in each sample separately; damaged seeds were counted jointly in 30 samples. In the identification of the seeds the seed collection of the Botanical Garden of the University of Warsaw was used, as well as botanical guides and atlases Bertsch (1941), Beijerinck (1947), Brouwer and Stählin (1955), Martin and Barkley (1961).

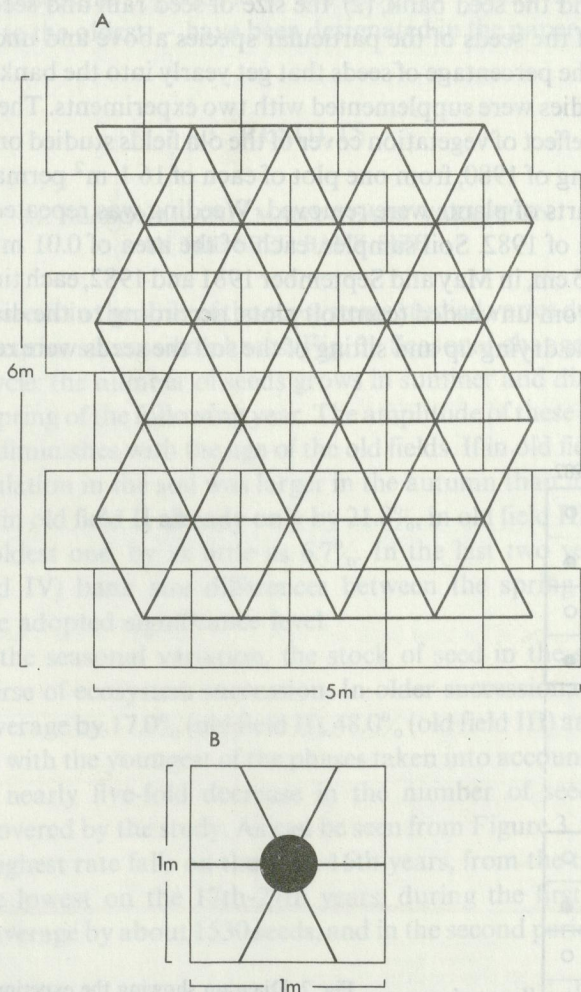


Fig. 1. Diagram of sample collecting

A — grid of shifted squares, B — sampling spot within a square

Then the average number was calculated of seeds per unit soil area, and the percentages of the particular species in the bank as a whole. The horizontal spatial structure type of the seed bank was determined on the basis of isarithmic charts prepared by the mathematical interpolation method (K o c i m o w s k i and K w i a t e k 1976). To describe the vertical bank distribution percentage of all the seeds occurred in the successive, two-centimetre soil layers was determined.

The species composition of the phytocoenoses in the consecutive succession phases, the population size of each species and the number of fruiting individuals were assessed each year in permanent plots, each of the size of 2 m × 32 m. Subsequently, outside the plots, for each species the individual diaspore production was assessed, on the basis of which the size was estimated of the seed rain falling during a year onto 1 m² of soil. These data made it possible to compare: (1) the floristic composition of the phytocoenosis and the seed bank, (2) the size of seed rain and seed bank, and (3) the numeric ratios of the seeds of the particular species above and under the soil surface, and to estimate the percentage of seeds that get yearly into the bank from the seed rain.

The main studies were supplemented with two experiments. The aim of one of them was to assess the effect of vegetation cover of the old fields studied on the size of the seed bank. In the spring of 1980, from one plot of each of 16 1 m² permanent plot pairs the above-ground parts of plants were removed. Weeding was repeated 2–3 times a year until the autumn of 1982. Soil samples, each of the area of 0.01 m², were collected at depths of 0.5–2.5 cm, in May and September 1981 and 1982, each time 16 samples from weeded and 16 from unweeded (control) plots, according to the diagram presented in Figure 2. After the drying up and sifting of the soil the seeds were removed from it and counted.

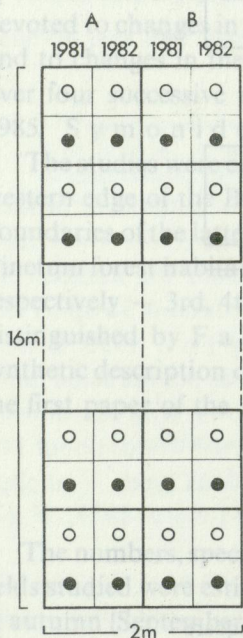


Fig. 2. Diagram showing the experimental plots
A – unweeded plots (control), B – weeded plots; open circles – samples collected in May, solid circles – samples collected in September

The objective of the other experiment was to estimate the germinating capability of the bank seeds, and to determine the effect of the depth of deposition of the seeds on their germination. In May and September 1980, from each old field 6 additional, random soil samples were collected, each of a unit area of 0.1 m^2 , only from the depths of 0.5–2.5 cm. The soil of each sample was mixed thoroughly and then divided into two equal parts and transferred to trays of the size of 19.5 cm by 25.6 cm. Into one tray of each pair a half-centimetre layer of pure sand was additionally poured, and into the other one a two and a half-centimetre layer of pure sand. All the trays were placed in a cool green-house for 8 weeks, throughout which a constant soil moisture was maintained. Every 4–5 days the seedlings that emerged were counted and identified by means of Häfliger and Brun-Hool's (1971) atlas.

All the results have been calculated per 1 m^2 of soil, and in the determination of the significance of differences the 5% odds level was adopted. The old fields under study – from the youngest to the oldest – have been designated in the paper with the numbers I, II, III and IV.

3. RESULTS

3.1. SEASONAL AND MANY-YEARS' VARIATION IN THE SEED BANK SIZE

The number of seeds in the soils of the ecosystems studied varies during the year and between the consecutive succession phases (Fig. 3). Seasonal changes in the bank size follow a regular cycle: the number of seeds grows in summer and diminishes from the autumn until the spring of the following year. The amplitude of these oscillations, at first very wide, clearly diminishes with the age of the old fields. If in old field I, the youngest one, the seed population in the soil was larger in the autumn than in the spring on an average by 37.8%, in old field II already only by 21.8%, in old field III by 14.4%, and in old field IV, the oldest one, by as little as 6.7%. In the last two years of the period analysed (old field IV) bank size differences between the spring and autumn are insignificant at the adopted significance level.

Regardless of the seasonal variation, the stock of seed in the surface soil layers shrinks in the course of ecosystem succession. In older successional phases the bank was lower on an average by 17.0% (old field II), 48.0% (old field III) and 79.4% (old field IV) in comparison with the youngest of the phases taken into account. This means that there occurred a nearly five-fold decrease in the number of seeds during the 21 succession years covered by the study. As can be seen from Figure 3, the rate of this fall is not even. The highest rate falls on the 11th-16th years, from the time of cultivation cessation, and the lowest on the 17th-27th years; during the first period the bank diminishes on an average by about 1530 seeds, and in the second period – by 869 seeds per 1 m^2 of soil.

The number of seeds accumulated in the soil was much smaller than the number of seeds falling down on the soil throughout the period analysed, and the seed rain to seed

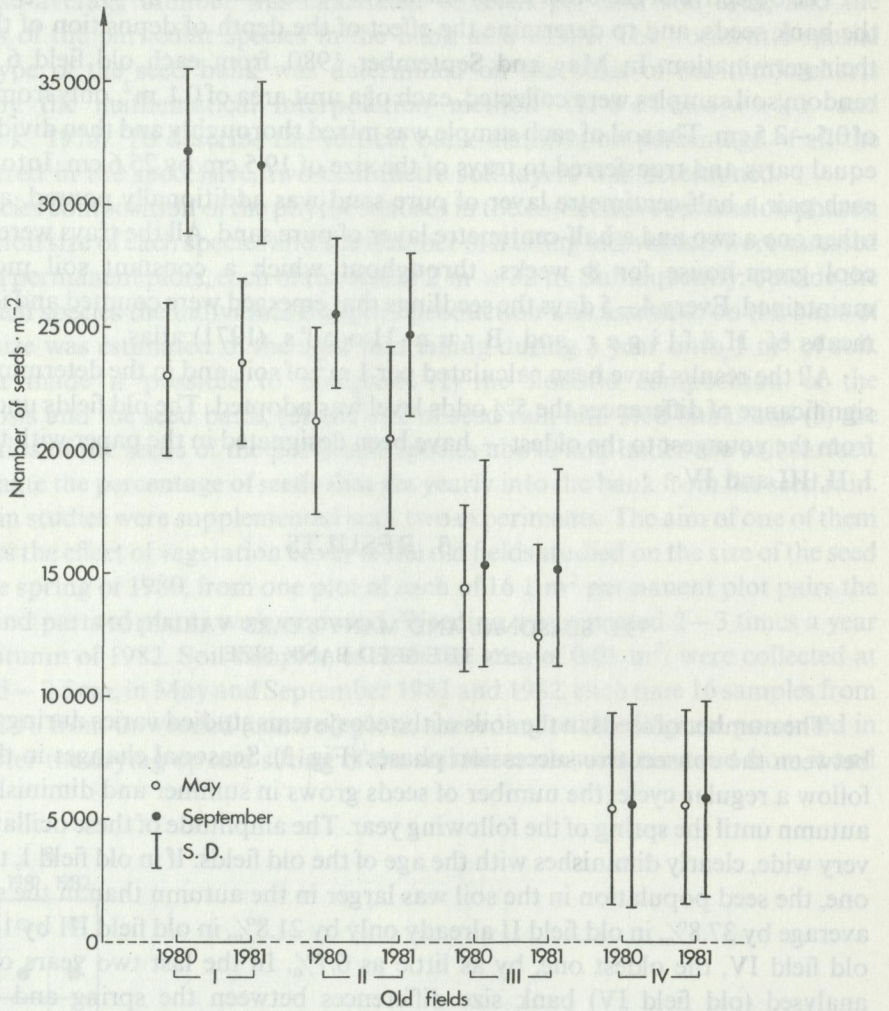


Fig. 3. Variation of the seed bank size during the year and in the course of succession

Table 1. Comparison of the seed rain and the seed bank in the soil (two-years' mean values)

Old field	Seed rain (per m ²)	Seed bank (per m ²)	Seed rain : seed bank (%)	Seed rain addition to the bank (%)
I	103728.5 ± 9720	27673.3 ± 5079	3.75 ± 1.2	8.47 ± 0.59
II	123210.0 ± 10107	22977.5 ± 2648	5.36 ± 2.1	3.66 ± 0.08
III	119688.0 ± 10878	14390.0 ± 1397	8.30 ± 2.9	1.62 ± 1.13
IV	70102.5 ± 5212	5700.8 ± 216	12.30 ± 3.7	0.57 ± 0.07

bank ratio increases in the course of succession several-fold (Table 1). This is the result primarily of the ever-decreasing percentage of seed penetrating deep down the soil profile from the surface. For the size of seed rain for many years varies over a relatively

narrow range (old fields I, II and III), clearly decreasing, and not growing, in the last phase (Table 1).

While the number of seeds in the soil differs significantly between the particular old fields, the proportion of damaged seeds is similar, always very low, not exceeding 1.4% of the entire bank. For this reason damaged seeds were not taken into account in the summaries of results concerning the seed bank.

3.2. EFFECT OF THE PLANT COVER ON THE SIZE OF THE SEED BANK

The results from the experiment aimed at establishing the effect of the plant cover of the old fields studied on the number of seeds penetrating into the soil have confirmed the supposition that there is no close relationship between the seed rain and seed bank. The removal of the above-ground parts of plants from the experimental plots resulted already in the following year in a growth in the seed bank size in comparison with the seed bank in the control plot soil, evident in all the old fields. At the end of the 2-year weeding differences between the weeded and the unweeded plots appeared to have increased (Fig. 4).

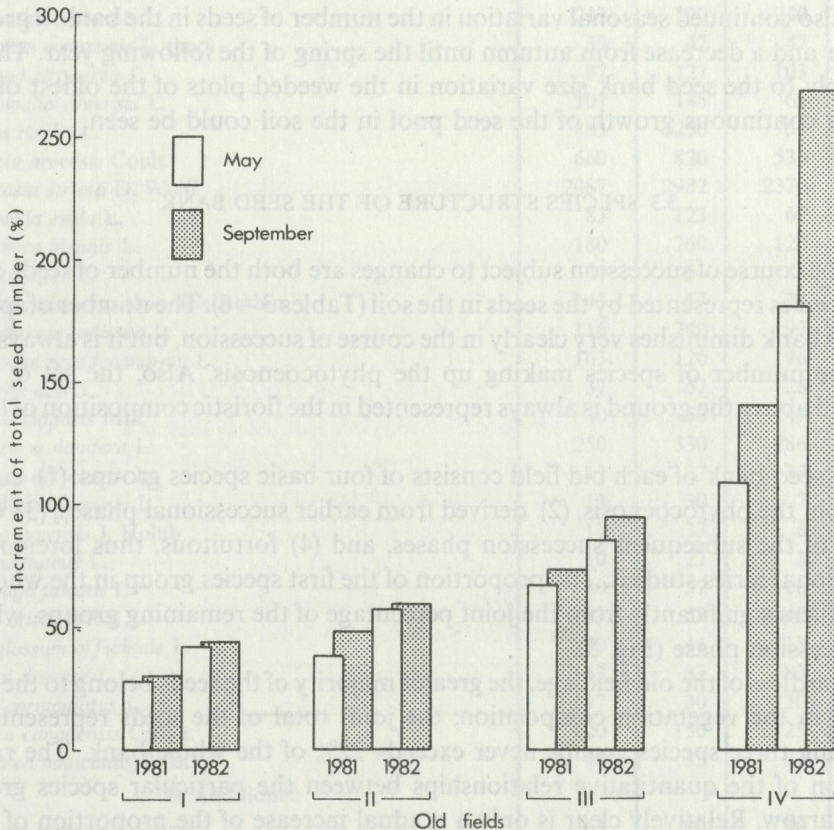


Fig. 4. Percentage increment of the weeded plot seed bank size related to control plot bank size

Uncovering the soil surface appeared to have had a variable effect on the seed input into the soil of the old fields compared. The effect of weeding depended on the old field age, the older the field, the greater the effect, being finally over six times as great in old field IV as in old field I (Fig. 4).

Table 2. Size of the seed bank after plant cover removal

Old field	Seeds · m ⁻²			
	1981		1982	
	April	September	April	September
I	31950.0 ± 2629	42687.5 ± 2347	32462.5 ± 3669	44569.0 ± 1704
II	28156.0 ± 3102	37362.5 ± 1547	29568.7 ± 1961	38018.7 ± 3049
III	21200.0 ± 3509	27956.3 ± 4599	24012.5 ± 2985	28568.7 ± 4539
IV	11775.0 ± 1384	14212.5 ± 1142	15762.5 ± 1665	21643.7 ± 2566

Seed bank size differences between the old fields representing consecutive succession phases, although much smaller after weeding, were still significant (Table 2). There also continued seasonal variation in the number of seeds in the bank: a growth in summer and a decrease from autumn until the spring of the following year. This does not apply to the seed bank size variation in the weeded plots of the oldest old field, where a continuous growth of the seed pool in the soil could be seen.

3.3 SPECIES STRUCTURE OF THE SEED BANK

In the course of succession subject to changes are both the number of seeds and the list of species represented by the seeds in the soil (Tables 3 – 6). The number of species in the seed bank diminishes very clearly in the course of succession, but it is always higher than the number of species making up the phytocoenosis. Also, the set of species recorded above the ground is always represented in the floristic composition of the seed bank.

The seed bank of each old field consists of four basic species groups: (1) currently present in the phytocoenosis, (2) derived from earlier successional phases, (3) characteristic of the subsequent succession phases, and (4) fortuitous, thus foreign to the successional series studied. The proportion of the first species group in the whole seed bank differs significantly from the joint percentage of the remaining groups, whatever the succession phase (Fig. 5).

Regardless of the old field age, the greater majority of the seeds belong to the species present in the vegetation composition; the joint total of the seeds representing the remaining three species groups never exceeds 22% of the whole bank. The range of variation of the quantitative relationships between the particular species groups is fairly narrow. Relatively clear is only a gradual increase of the proportion of species occurring in the later succession phases, and — less marked — a decrease in the

Table 3. Species represented in the seed bank and their contribution to it (old field I)

Species	Seeds · m ⁻²			
	1980		1981	
	Apr.	Sept.	Apr.	Sept.
1	2	3	4	5
A. Present in phytocoenosis:				
<i>Corynephorus canescens</i> Beauv.	6227	7956	5890	9466
<i>Hieracium pilosella</i> L.	4550	6487	4940	6867
<i>Helichrysum arenarium</i> Moench	2417	3050	1803	2340
<i>Festuca rubra</i> L.	1056	1927	1330	1753
<i>Agrostis tenuis</i> Sibth.	453	1226	490	1010
<i>Hypericum perforatum</i> L.	377	473	453	517
<i>Jasione montana</i> L.	587	1040	637	817
<i>Artemisia vulgaris</i> L.	320	483	263	357
<i>Achillea millefolium</i> L.	197	260	160	220
<i>Centaurea rhenana</i> Bor.	160	207	130	87
<i>Rumex acetosella</i> L.	253	320	200	196
<i>Scleranthus perennis</i> L.	217	290	240	320
<i>Juniperus communis</i> L. (juv.)	30	47	47	70
<i>Solidago virgaurea</i> L.	87	127	103	130
<i>Convolvulus arvensis</i> L.	107	146	63	80
<i>Holcus mollis</i> L.	883	1250	757	1230
<i>Knautia arvensis</i> Coult.	660	820	536	603
<i>Euphrasia stricta</i> D. Wolff.	2087	2987	2370	2726
<i>Euphorbia esula</i> L.	83	123	63	70
<i>Oenothera biennis</i> L.	180	260	120	157
<i>Viola tricolor</i> L.	30	56	16	27
<i>Chamaecytisus ratisbonensis</i> Rothm.	43	57	24	16
<i>Hypochoeris radicata</i> L.	116	240	97	303
<i>Cerastium semidecandrum</i> L.	163	120	196	57
<i>Erigeron acer</i> L.	37	57	26	30
<i>Linaria vulgaris</i> Mill.	40	50	47	10
<i>Agrostis stolonifera</i> L.	250	330	286	363
<i>Anchusa officinalis</i> L.	13	27	37	13
<i>Anthyllis vulneraria</i> L.	13	30	7	37
<i>Logfia arvensis</i> J. Holub	17	33	6	23
<i>Lupinus luteus</i> L.	10	27	3	7
<i>Medicago falcata</i> L.	30	37	16	10
<i>Silene otites</i> Wibel	33	57	40	33
<i>Cynoglossum officinale</i> L.	30	46	13	24
<i>Thlaspi arvense</i> L.	143	87	83	36
<i>Lotus corniculatus</i> L.	37	30	30	27
<i>Conyza canadensis</i> Crong.	120	150	123	47
<i>Teesdalea nudicaulis</i> , R. Br.	40	33	27	26
B. Additional:				
<i>Trifolium campestre</i> Schreb.	63	90	36	66
<i>Scleranthus annuus</i> L.	140	126	116	97

Table 3 continued

1	2	3	4	5
<i>Viola arvensis</i> Murr.	30	37	27	20
<i>Sinapis arvensis</i> L.	37	53	33	27
<i>Arabidopsis thaliana</i> Heynh.	77	74	74	56
<i>Anthemis arvensis</i> L.	97	103	63	113
<i>Stachys annua</i> L.	40	43	36	33
<i>Galeopsis ladanum</i> L.	93	107	103	50
<i>Veronica dillenii</i> Cr.	116	104	123	57
<i>V. verna</i> L.	143	140	97	63
<i>Myosotis micrantha</i> Pall.	30	43	23	24
<i>Arnoseris minima</i> Schweig.	43	33	33	13
<i>Fagopyrum sagittatum</i> Gilib.	63	53	64	30
<i>Digitaria ischaemum</i> Muehlenb.	130	137	130	87
<i>Spergula arvensis</i> L.	120	123	120	80
<i>Gypsophila muralis</i> L.	70	83	70	56
<i>Poa compressa</i> L.	43	36	43	33
<i>Raphanus raphanistrum</i> L.	37	43	37	27
<i>Silene alba</i> E. H. L. Krause	33	13	20	3
<i>Capsella bursa-pastoris</i> Med.	—	30	36	6
<i>Betula verrucosa</i> Ehrh.	56	153	57	187
<i>Populus tremula</i> L.	61	50	13	70
<i>Pinus sylvestris</i> L.	157	153	197	183

proportion of the species making up the plant community of the old fields studied (Fig. 5).

The number of species, the seeds of which represent over 5% of the seed bank is not high, varying between two and six in the different succession phases. However, the group of dominants distinguished on the basis of this criterion includes from 44.0 to 72.6% of the whole seed pool in the soil (Fig. 6). The absolute dominant in the seed bank is either *Corynephorus canescens* (in old fields I and III), or *Hieracium pilosella* (in old fields II and IV). Only four other species complete the list of dominants, with *Spergula morisonii* occurring only in old field III. It must be emphasized that four of the six dominant species of the seed bank occurred in the composition of the phytocoenoses throughout the succession period analysed (Tables 3–6, Fig. 6).

Scarce, relatively, is the number of subdominants distinguished on the basis of a 3–5% proportion in the whole seed bank. It varies between one (old fields I and II) and 7 (old field IV). The list of subdominants contains a total of only 12 species. Six of the species: *Festuca rubra*, *Agrostis tenuis*, *Jasione montana*, *Calluna vulgaris*, *Thymus serpyllum* and *Gypsophila fastigiata* remain subdominant in at least two of the four old fields studied.

Most numerous group throughout the succession period is the species representing a very small proportion of the seeds in the bank. By contrast to the groups of dominants and subdominants, the floristic composition of this group is subject to significant changes during the succession. A numerous weed group retreats from the seed bank to

Table 4. Species represented in the seed bank and their contribution to it (old field II)

Species	Seeds · m ⁻²			
	1980		1981	
	Apr.	Sept.	Apr.	Sept.
A. Present in phytocoenosis:				
<i>Corynephorus canescens</i> Beauv.	4130	4634	2683	3583
<i>Hieracium pilosella</i> L.	5817	6213	4157	4580
<i>Helichrysum arenarium</i> Moench	1893	2620	2223	2680
<i>Festuca rubra</i> L.	1187	2093	1897	2254
<i>Agrostis tenuis</i> Sibth.	473	596	560	683
<i>Hypericum perforatum</i> L.	423	456	473	316
<i>Jasione montana</i> L.	483	750	563	1117
<i>Artemisia vulgaris</i> L.	250	307	283	350
<i>Achillea millefolium</i> L.	220	250	193	273
<i>Centaurea rhenana</i> Bor.	123	83	140	63
<i>Rumex acetosella</i> L.	273	263	217	257
<i>Scleranthus perennis</i> L.	197	317	250	296
<i>Juniperus communis</i> L.	80	130	140	120
<i>Solidago virgaurea</i> L.	150	317	117	340
<i>Convolvulus arvensis</i> L.	170	130	157	67
<i>Holcus mollis</i> L.	703	927	820	1023
<i>Knautia arvensis</i> Coult.	253	220	197	157
<i>Euphrasia stricta</i> D. Wolff	1877	2420	1827	2703
<i>Euphorbia esula</i> L.	57	50	36	47
<i>Oenothera biennis</i> L.	126	63	90	130
<i>Viola tricolor</i> L.	47	24	36	47
<i>Chamaecytisus ratisbonensis</i> Rothm.	47	7	20	6
<i>Hypochoeris radicata</i> L.	160	293	170	317
<i>Cerastium semidecandrum</i> L.	270	130	357	97
<i>Erigeron acer</i> L.	50	156	120	170
<i>Thymus serpyllum</i> L.	203	373	316	423
<i>Carlina vulgaris</i> L.	117	140	150	130
<i>Calluna vulgaris</i> Hull.	220	156	170	200
<i>Teesdalea nudicaulis</i> R. Br.	63	36	53	50
B. Additional:				
<i>Linaria vulgaris</i> Mill.	27	24	30	27
<i>Agrostis stolonifera</i> L.	113	70	83	100
<i>Thlaspi arvense</i> L.	94	53	104	96
<i>Scleranthus annuus</i> L.	120	70	74	90
<i>Sinapis arvensis</i> L.	33	10	30	37
<i>Anthemis arvensis</i> L.	103	37	57	54
<i>Raphanus raphanistrum</i> L.	434	24	190	147
<i>Gypsophila fastigiata</i> L.	126	407	250	356
<i>Peucedanum oreoselinum</i> Moench	164	206	247	284
<i>Galium verum</i> L.	84	104	160	190
<i>Betula verrucosa</i> Ehrh.	77	70	160	250
<i>Populus tremula</i> L.	37	56	124	226
<i>Salix aurita</i> L.	16	37	97	150
<i>S. rosmarinifolia</i> L.	30	44	86	183

Table 5. Species represented in the seed bank and their contribution to it (old field III)

Species	Seeds · m ⁻²			
	1980		1981	
	Apr.	Sept.	Apr.	Sept.
A. Present in phytocoenosis:				
<i>Corynephorus canescens</i> Beauv.	3670	4360	2750	3326
<i>Hieracium pilosella</i> L.	2717	3696	1520	1110
<i>Helichrysum arenarium</i> Moench	1083	147	920	1027
<i>Festuca rubra</i> L.	517	887	490	950
<i>Agrostis tenuis</i> Sibth.	297	484	370	520
<i>Hypericum perforatum</i> L.	150	287	107	264
<i>Jasione montana</i> L.	220	297	173	316
<i>Artemisia vulgaris</i> L.	84	157	120	97
<i>Achillea millefolium</i> L.	80	250	120	193
<i>Centaurea rhenana</i> Bor.	40	64	24	44
<i>Rumex acetosella</i> L.	83	153	116	187
<i>Scleranthus perennis</i> L.	247	330	293	357
<i>Juniperus communis</i> L.	150	190	170	220
<i>Solidago virgaurea</i> L.	87	120	83	103
<i>Convolvulus arvensis</i> L.	16	70	30	57
<i>Holcus mollis</i> L.	364	416	320	380
<i>Thymus serpyllum</i> L.	523	707	540	823
<i>Calluna vulgaris</i> Hull.	340	317	453	373
<i>Spergula morisonii</i> Boreau	707	149	917	1686
<i>Holcus lanatus</i> L.	250	344	273	376
<i>Teesdalea nudicaulis</i> R. Br.	70	30	37	16
B. Additional:				
<i>Knautia arvensis</i> Coult.	107	90	80	57
<i>Euphrasia stricta</i> D. Wolff.	1056	893	823	650
<i>Oenothera biennis</i> L.	43	30	36	33
<i>Agrostis stolonifera</i> L.	36	27	23	26
<i>Scleranthus annuus</i> L.	80	57	60	33
<i>Sinapis arvensis</i> L.	67	73	37	24
<i>Gypsophila fastigiata</i> L.	460	566	506	626
<i>Chamaecytisus ruthenicus</i> A. Klášková	3	24	20	34
<i>Galium mollugo</i> L.	70	90	64	116
<i>G. verum</i> L.	140	223	170	270
<i>Betula verrucosa</i> Ehrh.	110	113	123	170
<i>Populus tremula</i> L.	156	216	196	293
<i>Salix aurita</i> L.	37	57	53	107
<i>S. rosmarinifolia</i> L.	150	123	197	136
<i>S. caprea</i> L.	40	47	34	90
<i>Pinus sylvestris</i> L.	17	36	33	40

Table 6. Species represented in the seed bank and their contribution to it (old field IV)

Species	Seeds · m ⁻²			
	1980		1981	
	Apr.	Sept.	Apr.	Sept.
A. Present in phytocoenosis:				
<i>Corynephorus canescens</i> Beauv.	1097	1610	1330	1007
<i>Hieracium pilosella</i> L.	1340	1706	1517	1553
<i>Helichrysum arenarium</i> Moench	247	196	204	273
<i>Festuca rubra</i> L.	150	187	127	140
<i>Agrostis tenuis</i> Sibth.	127	157	97	140
<i>Hypericum perforatum</i> L.	37	74	30	56
<i>Jasione montana</i> L.	140	217	123	193
<i>Artemisia vulgaris</i> L.	64	83	57	103
<i>Achillea millefolium</i> L.	23	36	57	27
<i>Centaurea rhenana</i> Bor.	7	16	17	30
<i>Rumex acetosella</i> L.	36	63	24	43
<i>Scleranthus perennis</i> L.	90	116	64	83
<i>Juniperus communis</i> L.	210	223	160	240
<i>Teesdalea nudicaulis</i> R. Br.	150	90	130	64
<i>Thymus serpyllum</i> L.	130	140	123	120
<i>Calluna vulgaris</i> Hull.	170	180	160	207
<i>Spergula morisonii</i> Boreau	106	157	84	120
<i>Holcus lanatus</i> L.	83	120	63	127
<i>Astragalus arenarius</i> L.	17	37	7	24
<i>Nardus stricta</i> L.	36	70	24	97
B. Additional:				
<i>Solidago virgaurea</i> L.	43	34	24	36
<i>Knautia arvensis</i> Coult.	16	13	30	10
<i>Euphrasia stricta</i> D. Wolff.	243	196	207	156
<i>Hypochoeris radicata</i> L.	30	27	16	10
<i>Scleranthus annuus</i> L.	37	30	24	27
<i>Galium mollugo</i> L.	80	64	77	123
<i>G. verum</i> L.	117	106	140	117
<i>Betula verrucosa</i> Ehrh.	140	150	130	180
<i>Populus tremula</i> L.	163	194	170	207
<i>Salix aurita</i> L.	44	40	56	30
<i>S. rosmarinifolia</i> L.	120	107	97	117
<i>S. caprea</i> L.	63	43	47	70
<i>Pinus sylvestris</i> L.	20	17	33	24
<i>Vincetoxicum officinale</i> Mnch.	16	23	13	36

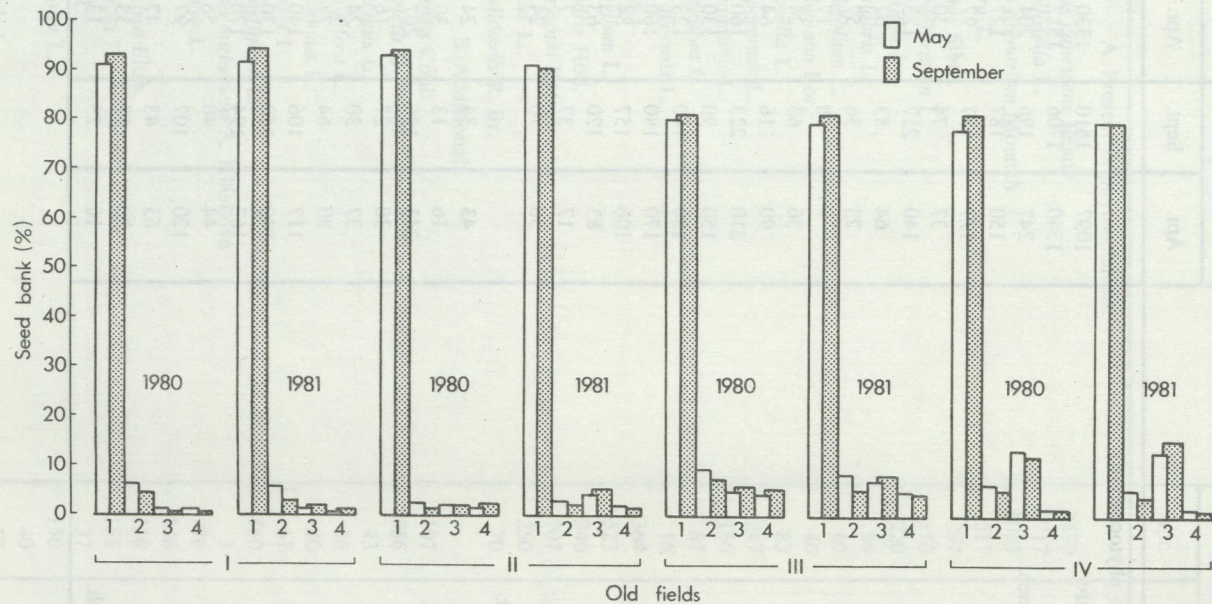


Fig. 5. Contribution of different species groups to the whole seed bank

1 – species present in the phytocoenosis, 2 – species derived from earlier successional phases, 3 – species characteristic of next successional phases, 4 – accidental species

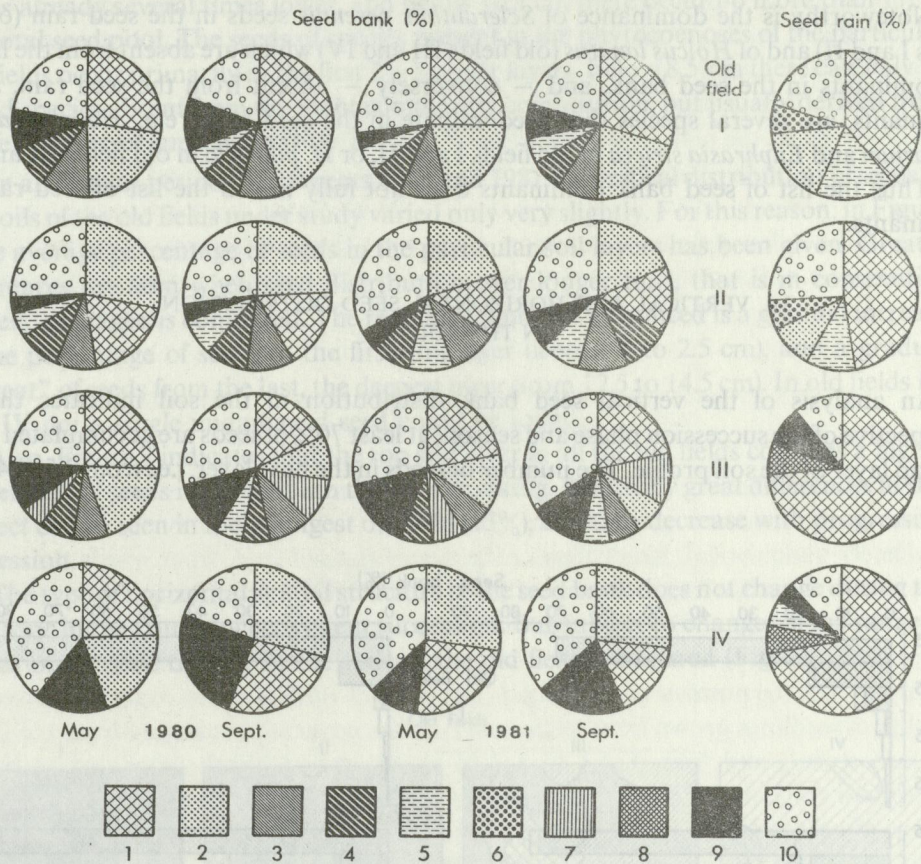


Fig. 6. Species structure of seed bank and seed rain

1 – *Corynephorus canescens*, 2 – *Hieracium pilosella*, 3 – *Helichrysum arenarium*, 4 – *Euphrasia stricta*, 5 – *Festuca rubra*, 6 – *Scleranthus perennis*, 7 – *Spergula morisonii*, 8 – *Holcus lanatus* (dominant; contribution > 5%), 9 – subdominants jointly (contribution 3–5%), 10 – other species (contribution < 3%)

be replaced with the seeds of trees, dwarf-shrubs and herbs specific to the late succession phases of the ecosystems studied (Tables 3–6). It must be noted here that the list of species representing a slight percentage of the seed bank is in reality longer by another 4–5 taxa, which could not, however, be identified.

The joint contribution to the seed bank of dominants, subdominants and the remaining group of species varies somewhat during the year, and so do the quantitative relationships within the dominant group. However, the changes are as a rule of the nature of small fluctuations.

Poorer than in the seed bank is the list of dominants in the seed rain (Fig. 6). Only 2–4 species account for more than 5% of the total pool of seeds falling on the ground. The absolute dominant in all old fields is *C. canescens*, whose contribution to the number of seeds in the seed rain grows with advancing plant community succession.

Noteworthy is the dominance of *Scleranthus perennis* seeds in the seed rain (old fields I and II) and of *Holcus lanatus* (old fields III and IV) which are absent from the list of dominants in the seed bank, and — conversely — absent from the seed rain, as dominants, are several species that predominate in the seed bank, e.g., *Helichrysum arenarium* and *Euphrasia stricta* in old fields I and II, or *H. pilosella* in old fields III and IV. Thus the list of seed bank dominants does not fully match the list of seed rain dominants.

3.4. VERTICAL AND HORIZONTAL SEED DISTRIBUTION IN THE SOIL

An analysis of the vertical seed bank distribution in the soil indicates that irrespective of the succession phase and season, at least 70% of seeds are accumulated in the top layer of the soil profile. The number of seeds in the next layer, i.e., from 2.5 to 4.5

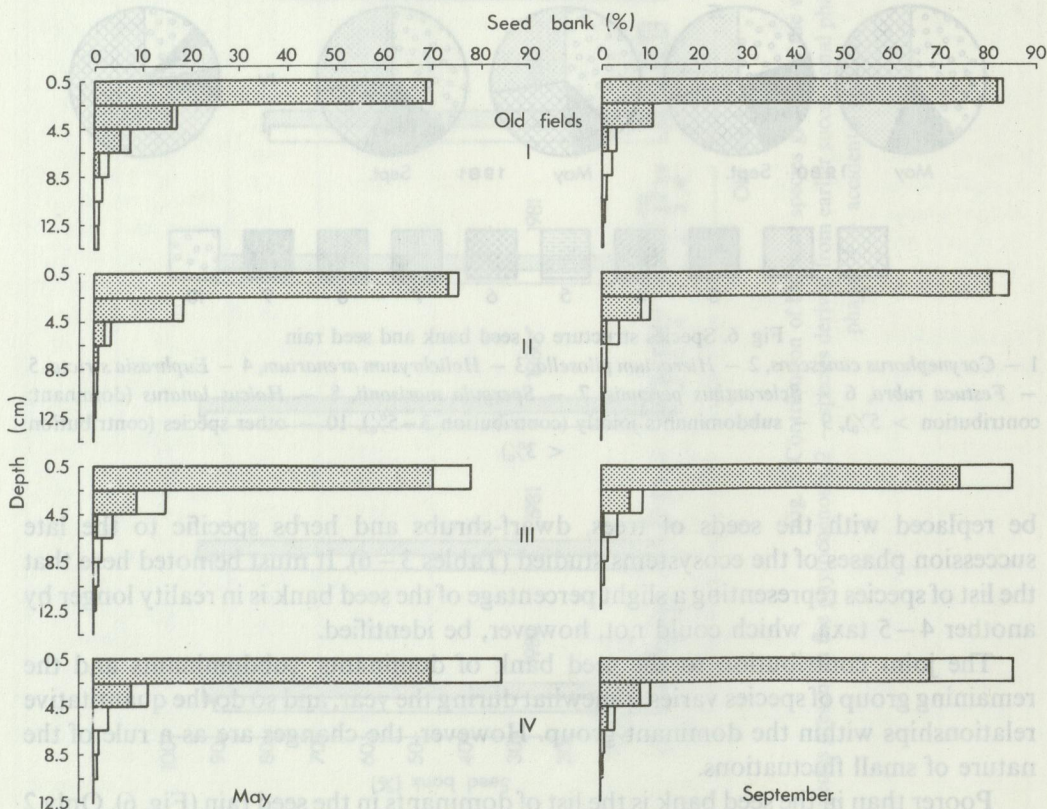


Fig. 7. Vertical spatial structure of the seed bank

Worked out on the basis of average values for two years; dark fields — seeds of species present in the phytocoenosis, light fields — seeds of the remaining three species groups (see Fig. 5)

cm, is already several times lower, and below 10.5 cm there occur no more than 1% of the total seed pool. The seeds of species present in the phytocoenoses of the particular old fields occur primarily in the first 2–3 upper layers. Below 8.5 cm there can only be found species absent from the plant community composition, but usually derived from earlier phases of succession (Fig. 7).

In analogous periods of the years 1980 and 1981 the vertical distribution of seeds in the soils of the old fields under study varied only very slightly. For this reason, in Figure 7 the average percentage of seeds in the particular soil layers has been given. Greater differences are seen when seed distribution over longer time, that is in consecutive succession stages, is compared. The regularity that can be noticed is a gradual increase of the percentage of seeds in the first soil layer (from 0.5 to 2.5 cm), and a gradual “retreat” of seeds from the last, the deepest layer (from 12.5 to 14.5 cm). In old fields III and IV not a single undamaged seed could be found.

Also, Figure 7 indicates that the top soil layer in all the old fields contains a higher percentage of seeds in the autumn than in the spring. Relatively great differences in this respect can be seen in the youngest old field (13%), and they decrease with progressing succession.

The type of horizontal spatial structure of the seed bank does not change during the year, nor in the course of ecosystem succession. But subject to changes is the range of values of the seed density in the soils of the old fields compared (Fig. 8).

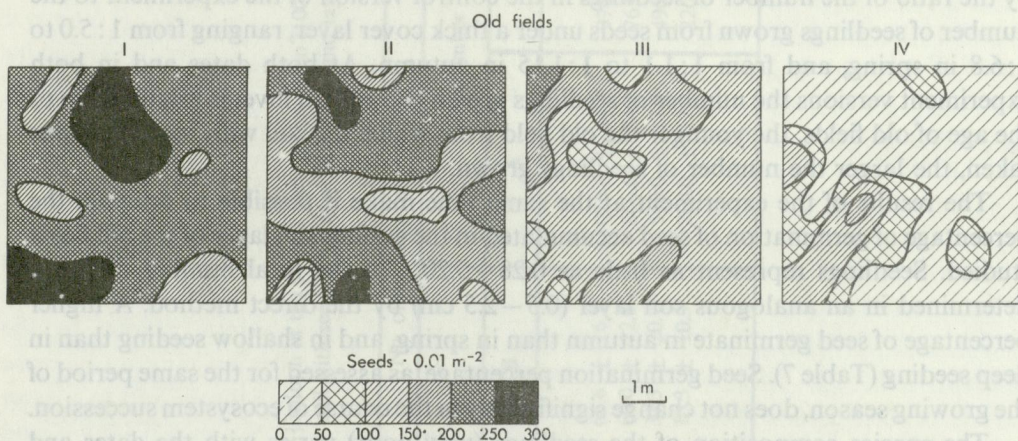


Fig. 8. Horizontal spatial structure of the seed bank
Spring, 1980

The interpolation map illustrating the spatial structure of the seed bank in the spring of 1980, as an example, shows that the degree of complexity of the mosaic of “aggregations” and “thinnings” is similar, regardless of the succession phase. Figure 8 also shows that the value of seed density in aggregations and thinnings, and the size of the area of the zones with a specified number of seeds change very clearly during the succession. It is for this reason that in old field I in the most thinned zones, jointly

comprising an area of about 4 m², the density of seeds ranges from 150 to 200 per 0.01 m² of soil, while in old field IV the range of these values is characteristic of the highest density, found only in one, small aggregation (Fig. 8).

Spatial structure changes in the seed bank during the year are of a nature similar to that observed in the course of succession. Regardless of the age of an old field, they consist only in an increase in density (in both the aggregation zones and thinning zones) during the summer, and a decrease in density in the period from the autumn to the spring of the following year. The degree of contrast between the zone of aggregations and the zone of thinnings, as well as their spatial relationships remain unchanged.

3.5. EFFECT OF THE DEPTH OF DEPOSITION OF THE SEED IN THE SOIL ON THEIR GERMINATION

The results obtained from the experiment carried out in order to estimate the chance of the seeds to germinate in relationship to their location in the soil are completely unequivocal. Regardless of the age of the old field, from which the seeds have been collected, a larger number of them germinate if they are located immediately below the soil surface (Table 7). The harmful effect of the two and a half-centimetre cover sand layer proved to be much stronger in spring than in autumn. This is indicated by the ratio of the number of seedlings in the control version of the experiment to the number of seedlings grown from seeds under a thick cover layer, ranging from 1:5.0 to 1:6.8 in spring, and from 1:1.1 to 1:1.15 in autumn. At both dates and in both experiment versions the number of seedlings grown showed an inverse relationship to the age of old fields, the younger the old field from which the soil with seeds in it was taken, the larger the number of seedlings grown.

The results of the experiment at the same time make it possible to estimate the percentage of germination of seed accumulated in the surface soil layer of the old fields studied. Seedlings represent as little as 0.28–5.20% of the total number of seeds, determined in an analogous soil layer (0.5–2.5 cm) by the direct method. A higher percentage of seed germinate in autumn than in spring, and in shallow seeding than in deep seeding (Table 7). Seed germination percentage, as assessed for the same period of the growing season, does not change significantly in the course of ecosystem succession.

The species composition of the seedlings (very poor) varies with the dates and experiment versions; the age of the old fields proved to be almost of no importance. In spring, in the control version there appeared seedlings of *H. pilosella*, representing 90–95% of the total number of seedlings, and 1–3 seedlings of each of the following: *F. rubra*, *A. tenuis*, *S. perennis*, *J. montana* and *A. millefolium*. In the deep seeding *H. pilosella* seedlings were accompanied only by single *F. rubra* seedlings. In autumn, regardless of the experiment version, only *C. canescens* diaspores (from the soil of old fields I and II), or *C. canescens* and *S. morisonii* diaspores (from the soil of old fields III and IV) germinated; however, the proportion of *S. morisonii* seedlings did not exceed 1.3%.

Table 7. Impact of the depth of seed location in the soil on their germination (100% – seed number in 0.5–2.5–centimetre soil layer counted directly)
 A – soil with seeds covered with a pure-sand layer of 0.5 cm and B – with of 2.5 cm

Old field	No. of seedlings · m ⁻²				Per cent of germination			
	April		September		April		September	
	A	B	A	B	A	B	A	B
I	380.0 ± 28.2	66.6 ± 16.3	1076.6 ± 34.4	976.6 ± 36.7	2.36	0.41	4.02	3.64
II	300.0 ± 17.9	60.0 ± 12.6	866.6 ± 24.2	763.2 ± 23.4	1.89	0.38	3.99	3.52
III	216.7 ± 15.1	33.3 ± 20.7	540.0 ± 17.9	490.0 ± 21.0	1.92	0.30	4.30	3.95
IV	90.0 ± 10.9	13.3 ± 10.3	260.0 ± 17.9	226.6 ± 24.2	1.92	0.28	5.19	4.53

4. DISCUSSION

A decrease in the number of seeds in the bank with the advancing age of the old fields has several times been reported on in the relevant literature, but it has usually been attributed to a decrease in the proportion of therophytes in the vegetation composition (N u m a t a et. al. 1964, L i v i n g s t o n e and A l l e s s i o 1968, H a r p e r 1977, K o n i a k and E v e r e t t 1982). In the soils of the old fields studied during the present series the numbers of seeds were determined by the same, small group of perennials, particularly *C. canescens* and *H. pilosella*, regardless of the age of the fields. The proportion of therophytes was never above 15% of the whole seed bank.

The seed bank decrease in the course of succession of the ecosystems studied did not result from a diminished seed rain quantity either. It suffices to say that compared with the youngest old field — field I, the number of seeds falling down on 1 m² of ground surface in old field III is greater by over 15 thousand, but the number of seeds accumulated in 1 m² of soil was over 13 thousand lower. The seed rain to seed bank ratio indicates that in the consecutive succession phases a smaller and smaller fraction of the diaspores produced by the plants penetrates down the soil profile.

Relatively little is known about the fate of diaspores that fall down onto the soil surface. It has been known that only a certain percentage of them, different in each ecosystem, forms the seed bank (R a b i n o w i t z and R a p p 1980, P e t r o v and B e l a e v a 1981, R a b i n o w i t z 1981). Part of the diaspores is carried by wind or animals out of the ecosystem boundaries. Some of them undergo a fast decomposition or fall a prey to herbivores (R a b o t n o v 1954, 1960, G e b c z y Ń s k a 1976). Finally, a proportion of them can germinate right away on the soil surface, without a resting period (T h o m p s o n and G r i m e 1979).

The disproportion, increasing in the course of succession of the old fields under study, between the seed rain and the seed bank is to a large extent caused by changes in the species structure of the vegetation, and particularly changes in the numerical ratio of the population of flowering plants to that of sporogenous plants. In the phytocoenoses of the consecutive succession phases there occurs a significant increase in the proportion of mosses, especially of *Polytrichum piliferum* Schreb., and to a lesser extent also of lichens, particularly those of the genus *Cladonia* (S y m o n i d e s and B o r o w i e c k a 1985). The joint sporogenous plant cover of the old field surface increased from 15% in the 6th succession year to 85% in the 26th year (S y m o n i d e s 1985). Moss and lichen cushions to a considerable degree impede seed access to the soil (S y m o n i d e s 1979). It is not surprising that after the removal of the vegetation cover in the experimental plots it was in old field IV that the highest increase in numbers of the seeds in the bank was found, the growth in other old fields being related to the field age, the younger the field, the lower the growth.

The question could be asked as to why the removal of the above-ground parts of plants did not result in a complete equalization of the seed number in the experimental plots of the particular old fields, at least those in which a similar quantity of seed rain

was found (I, II and III). Perhaps the time of the experiment was too short, and seed accumulation in the soil is usually a long-lasting process. An important role is probably played also by the change, in the course of succession, of the soil physical properties on which the percolation of rainfall water, and thereby the penetration of seed from the surface into the soil depend.

Hampered input of seeds into the soil, and their impeded germination on the surface, a large percentage of which is covered with moss and lichen cushions, account for the slower and slower rate of vegetation changes, and lengthening duration of the consecutive succession phases (F a l i ń s k i 1980). They also account, to some extent, for the growth of seasonal stability of the seed bank in the course of succession. In old field IV differences in the number of seeds between spring and autumn were very small, in spite of the strongly marked seasonality of the seed dispersal and diaspore germination of *C. canescens* — the absolute dominant of the seed rain and codominant of the seed bank (S y m o n i d e s 1979). As can be concluded from literature data, a seasonal seed bank stability of this kind is an exceptional phenomenon (cf. N u m a t a et al. 1964, T h o m p s o n and G r i m e 1979, P a v o n e and R e a d e r 1982, P i r o ż n i k o w 1983).

Many authors have stressed the fact that the number of seeds accumulated in the surface soil layers depends on the soil utilization, or on the species composition of the natural vegetation (G r i m e 1979, L e g u i z a m o n et al. 1981, F r o u d - W i l l i a m s et al. 1983). At the same time it has been known that, as in the case of the old fields under study, the size of the seed bank is usually determined only by a few species, not necessarily dominant in the seed rain (R a b i n o w i t z 1981, F r o u d - W i l l i a m s et al. 1983). The lack, found in the present study, of a close correspondence between the vegetation above the surface of a soil and the seed bank is a rule, regardless of the ecosystem type (O l m s t e d and C u r t i s 1947, M a j o r and P y o t t 1966, G r i m e 1979). It is also a regularity that the production of seed in an ecosystem is many times higher than the seed stock in the soil (H a r p e r 1977, G r i m e 1979).

The relationship between the vegetation and the seed bank in the particular old fields varies in the course of succession; what does not change is only the presence in the soil of seeds of all the species recorded in the phytocoenosis, and their numerical dominance in the seed bank as a whole. The richest floristic composition of the seed bank is found in the youngest old field, whereafter it grows poorer and poorer as the succession progresses, but the percentage of the plant community component species represented in the floristic composition of the seed bank fluctuates over a comparatively narrow range: from 58.9% to 67.0%, without any tendency towards directional changes. But subject to directional changes is the contribution of the species group considered to the total number of seeds in the bank, gradually diminishing with each subsequent succession phase.

The seed bank floristic composition reflects the species composition of the vegetation of both the earlier succession phases and earlier developmental stages of the plant community, and it also indicates the direction of further changes in the

phytocoenosis (K a r p o v 1969, H a r p e r 1977, T e m p l e t o n and L e v i n 1979). As in other succession series, in the old fields studied field-weed seeds continued to be present in the bank for a relatively long time, whereas the seeds of species characteristic of later successional phases, including some trees, appeared comparatively late (cf. L i v i n g s t o n e and A l l e s s i o 1968, A r c h i b o l d and H u m e 1983). The very low proportion of accidental species can be attributed to the floristic poverty of the ecosystems surrounding the old fields.

The vertical distribution of seeds in the soils appears to be similar in all the old fields: most of the seeds concentrate immediately beneath the soil surface, as they do in many other ecosystem types (C h i p p i n d a l e and M i l t o n 1934, M a j o r and P y o t t 1966, S y m o n i d e s 1978, Y a d a w and T r i p a t h i 1982). In the course of succession the percentage of seed accumulated in deeper soil layers diminishes, probably due to an impeded seed transport into the soil with the rainfall which is held back by mosses and lichens. The uneven horizontal seed distribution is the result of both the unequal chance to penetrate into the soil of seeds in different parts of a field, and a clumped distribution of the plants that have produced the seeds.

Experiments have demonstrated that out of the immense number of seeds accumulated in the surface soil layer of the particular old field several per cent, at the most, germinate each year. Under natural conditions the germinating fraction would probably be even smaller. This conclusion seems to be justified by the data reported by K r o p a č (1966), Barallis (1968, quoted after H a r p e r 1977), N a y l o r (1972) and many other authors, which indicate that in different ecosystems as little as 1–4% seeds germinate. The remainder of the seeds die or remain germinable for many years, depending on the biological properties of the plants, and properties of the soils (C h a p n e s s and M o r r i s 1948, K n a p p 1967, R o b e r t s 1970, R o b e r t s 1972, W e n t 1973, P e m a d a s a and L o v e l l 1974).

Experimental studies have also demonstrated that primarily seeds with a thin soil layer over them have the chance to germinate. It appears that the seeds of only a few species, like, e.g., *C. canescens* or *S. morisonii*, adapted to living on a mobile substrate, can germinate in a deeper layer.

To sum up, the studies have confirmed the truth of three of the four hypotheses formulated in the introduction, the verification of which was the main objective of the studies presented in the paper. In the course of a regenerative succession of a Peucedano-Pinetum forest there occurs a significant decrease in the number of species in the floristic composition of the seed bank, in the size of the latter, as well as in the seasonal variability of both of them. But no decrease was found in the proportion of species making up the phytocoenoses in the consecutive succession phases — either in respect of the presence in the seed bank composition of seeds of particular species, or in respect of their percentage. It may, however, be assumed that the development of a shrub layer in the course of further vegetation changes, and the retreat of light-demanding species (*C. canescens*, *P. piliferum*, *S. morisonii*) from the plant communities will bring about further significant qualitative and quantitative changes in the seed bank.

It is difficult to unequivocally answer the question asked in the introduction as to whether there is some correlation between the vegetation dynamics in the course of ecosystem succession and the dynamics of the seed bank. For some correlation may be indicated by the permanent presence in the seed bank of the set of species that make up the phytocoenoses and which do change in the consecutive phases, and by the gradually falling rate of changes in both the vegetation and seed bank. On the other hand, however, the response of the seed bank to changes taking place in the plant community is not immediate: proof of this is the presence in the seed bank of the seeds of a numerous group of species not present in the phytocoenosis any more. Likewise, there is some delay in the response of the phytocoenosis to changes in the species composition of the seed bank. All the species that enrich plant communities in the course of succession usually become components of the seed population in the soil at a much earlier stage.

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5. SUMMARY

The present study is part of comprehensive investigations into the dynamics of phytocoenoses, plant populations and biotope properties in the course of a secondary ecosystem succession in old fields. The aim of it was to analyse the: (1) size, species structure and spatial structure of the seed bank in the soils of uneven-aged old fields, (2) relationship between the seed rain and the seed bank in the course of ecosystem succession, (3) effect of the vegetation cover of the particular old fields on the number of seeds in the seed bank, and (4) germinability of the seed accumulated in the surface soil layer, in deep and shallow seeding.

The studies were carried out in the years 1980–1982 at the edge of the Białowieża Primaeval Forest, within its 16th-century boundaries. In the first study year the old fields, aged 6, 10, 16 and 26 years, represented according to F l i Ń s k i (1980), succession phases 3, 4, 5 and 6 of a Peucedano-Pinetum forest. In the paper they have been designated – respectively – with the figures I to IV. A description of the vegetation and soils can be found in the first paper of the series presented (S y m o n i d e s 1985).

The most important results from the studies can be presented in the following way:

- (1) The seed stock in the surface soil layers shrinks in the course of ecosystem succession; the amplitude also decreases of seasonal variation in the number of seeds in the bank (Fig. 3).
- (2) Regardless of the old-field age, the number of seeds in the soil is considerably lower than the number of seeds falling down onto the soil surface; the seed rain to seed bank ratio significantly increases with the consecutive succession phases (Table 1).
- (3) Uncovering the soil surface in experimental plots resulted in a growth in number of the seeds in the bank already in the following year, the older the old field, the more marked the growth (Fig. 4); but the differences between the old fields continued to be significant, even after two years' weeding (Table 2).
- (4) The number of species represented by seeds in the bank clearly diminishes in the course of succession, being, however, always higher than in the plant community. Throughout the study period the floristic composition of the seed bank contained the set of species recorded above the soil surface (Tables 3–6). Their seeds dominated numerically over the seeds of the remaining species (Fig. 5).

(5) The list of species dominant in the seed bank changes slightly with the consecutive succession phases, and it does not fully match the list of species dominant in the seed rain (Fig. 6).

(6) The type of vertical and horizontal spatial structure of the seed bank is similar in all the old fields compared. In the course of succession there occurs a slight increase in the percentage of seeds in the surface soil layer (from 0.5 to 2.5 cm), and a decrease in density of the seeds in the zones of aggregations and thinnings (Figs. 7, 8).

(7) The per cent germination of the seeds accumulated in the soils is very low, regardless of the old-field age, being similar in the analogous seasons. A higher percentage of seeds germinate in autumn than in spring, and in shallow seeding than in deep seeding (Table 7).

The results obtained from the studies suggest that the decrease in number of the seeds in the bank, and a fall of the rate of successional changes in the vegetation in the consecutive phases are mainly caused by an increased percentage of mosses (especially *Polytrichum piliferum*) and lichens (especially those of the genus *Cladonia*) in the community composition. Their cushions, tightly covering the soil surface, make difficult both the recruitment of seeds to the bank and their germination.

6. POLISH SUMMARY

Praca jest częścią szerszych studiów poświęconych dynamice fitocenozy, populacji roślinnych oraz właściwości biotopu w toku wtórnej sukcesji ekosystemów na gruntach porolnych. Jej celem była analiza: 1) liczebności, struktury gatunkowej i struktury przestrzennej banku nasion w glebach różnowiekowych ugorów, 2) związków między deszczem nasion a bankiem nasion w toku sukcesji ekosystemów, 3) wpływu pokrywy roślinnej poszczególnych ugorów na liczebność banku nasion oraz 4) zdolności kiełkowania nasion zalegających w powierzchniowej warstwie gleby, w warunkach płytkiego i głębokiego siewu.

Badania przeprowadzono w latach 1980–1982 na skraju Puszczy Białowieskiej, w jej historycznych granicach z XVI w. Ugorzy w wieku 6, 10, 16 i 26 lat w pierwszym roku badań reprezentują według F a l i n s k i e g o (1980) trzecią, czwartą, piątą i szóstą fazę sukcesji boru *Peucedano-Pinetum*. W pracy ponumerowano je cyframi – odpowiednio – od I do IV. Charakterystykę roślinności i gleb podano w pierwszej pracy prezentowanego cyklu (S y m o n i d e s 1985).

Najistotniejsze wyniki badań można ująć następująco:

1. Zapas nasion w powierzchniowych warstwach gleby kurczy się w toku sukcesji ekosystemów; zmniejsza się także amplituda sezonowych wahań liczebności banku nasion (rys. 3).

2. Niezależnie od wieku ugorów liczba nasion w glebie jest znacznie niższa od liczby nasion osypujących się na powierzchnię gleby; stosunek deszczu nasion do banku nasion istotnie wzrasta w kolejnych fazach sukcesji (tab. 1).

3. Odsłonięcie powierzchni gleby na poletkach eksperymentalnych spowodowało znaczny wzrost liczebności banku nasion już w następnym roku i to tym wyraźniejszy, im starszy był ugor (rys. 4); różnice pomiędzy ugorami pozostały jednak nadal istotne, nawet po 2 latach zabiegów pielenia (tab. 2).

4. Liczba gatunków reprezentowanych przez nasiona w banku wyraźnie maleje w toku sukcesji, zawsze jednak jest wyższa niż w zbiorowisku roślinnym. W całym okresie objętym badaniami na liście florystycznej banku nasion znajduje się komplet gatunków zarejestrowanych nad powierzchnią gleby (tab. 3–6). Ich nasiona przeważają liczebnie nad nasionami pozostałych gatunków (rys. 5).

5. Lista gatunków dominujących w banku nasion zmienia się nieznacznie w kolejnych fazach sukcesji, przy czym nie jest ona całkowicie zgodna z listą gatunków dominujących w deszczu nasion (rys. 6).

6. Typ pionowej i poziomej struktury przestrzennej banku nasion jest podobny na porównywanych ugorach. W toku sukcesji wzrasta nieco udział nasion w powierzchniowej warstwie gleby (od 0.5 do 2.5 cm) oraz maleje zagęszczenie nasion w strefach skupień i rozrzedzeń (rys. 7, 8).

7. Procent kiełkowania nasion zalegających w glebach jest bardzo niski, niezależnie od wieku ugoru, i podobny w analogicznych porach roku. Nasiona kiełkują w wyższym procencie jesienią niż wiosną i w warunkach płytszego niż głębszego siewu (tab. 7).

Wyniki badań sugerują, że spadek liczebności banku nasion oraz spadek tempa sukcesyjnych przemian roślinności w kolejnych fazach są spowodowane przede wszystkim wzrastającym udziałem mchów (zwłaszcza *Polytrichum piliferum*) i porostów (zwłaszcza z rodzaju *Cladonia*) w składzie zbiorowisk. Ich poduchy, szczególnie pokrywające powierzchnię gleby, utrudniają zarówno dopływ nasion do banku, jak też ich kiełkowanie.

7. REFERENCES

1. Archibold O. W., Hume L. 1983 — A preliminary survey of seed input into fallow fields in Saskatchewan (Canada) — *Can. J. Bot.* 61: 1216–1221.
2. Beijerinck W. 1947 — Zadenatlas der Nederlandsche flora — H. Veenman and Zonen, Wageningen, 316 pp.
3. Bertsch K. 1941 — Früchte und Samen. Ein Bestimmungsbuch zur Pflanzenkunde der vorgeschichtlichen Zeit — Verlag Ferdinand Enke, Stuttgart, 247 pp.
4. Brenchley W. E., Warrington K. 1930 — The weed seed population of arable soil. II. Influence of crop, soil, and methods of cultivation upon the relative abundance of viable seeds — *J. Ecol.* 21: 103–127.
5. Brenchley W. E., Warrington K. 1945 — The influence of periodic fallowing on the prevalence of viable weed seeds in arable soil — *Ann. appl. Biol.* 32: 285–296.
6. Brouwer W., Stählin A. 1955 — Handbuch der Samenkunde für Landwirtschaft, Gartenbau und Forstwirtschaft — DLG — Verlagsgesellschaft mbH, Frankfurt, 635 pp.
7. Chapness S. S., Morris K. 1948 — The population of buried viable weed seeds in relation to contrasting pasture and soil types — *J. Ecol.* 36: 149–173.
8. Chippindale H. G., Milton W. E. J. 1934 — On the viable seeds present in the soil beneath pastures — *J. Ecol.* 22: 508–531.
9. Falińska K. 1981 — Eksperymentalne badania biologii populacji wieloletnich roślin zielnych [Experimental studies of perennial plant populations] — *Wiad. bot.* 25: 209–230.
10. Faliński J. B. 1980 — Vegetation dynamics and sex structure of the populations of pioneer dioecious woody plants — *Vegetatio*, 43: 23–38.
11. Frond-Williams R. J., Dvennan D. S. H., Chancellor R. J. 1983 — Influence of cultivation regime upon buried weed seeds in arable cropping systems — *J. appl. Ecol.* 20: 187–198.
12. Gębczyńska Z. 1976 — Food habits of the bank vole and phenological phases of plants in an oak hornbeam forest — *Acta theriol.* 21: 223–236.
13. Grime J. P. 1979 — Plant strategies and vegetation processes — John Willey and Sons, Chichester — New York — Brisbane — Toronto, 222 pp.
14. Häfliger E., Brun-Hool J. 1971 — Weed communities of Europe — CIBA — GEIGY Limited, Basle, Switzerland.
15. Harper J. L. 1977 — Population biology of plants — Academic Press, London — New York — San Francisco, 892 pp.
16. Karpov V. G., 1969 — Éksperimentalnaja fitosociologija tiemnochvojnoj tajgi — Izd. Nauka, Leningrad, 230 pp.
17. Knapp R. 1967 — Experimentelle Soziologie und gegenseitige Beeinflussung der Pflanzen — Eugen Ulmer, Stuttgart, 266 pp.
18. Kocimowski K., Kwiatek J. 1976 — Wykresy i mapy statystyczne [Statistical maps and diagrams] — GUS, Warszawa, 155 pp.
19. Koniak S., Everett R. L. 1982 — Seed reserves in soils of successional stages in pinyon (*Pinus monophylla*) woodlands — *Am. midl. Nat.* 108: 295–303.
20. Kropač Z. 1966 — Estimation of weed seeds in arable soil — *Pedobiologia*, 6: 105–128.
21. Leguizamón E. S., Cruz P. A., Guíamet J. J., Casano L. M. 1981 — Weed seed bank determination in Pujato District (Santa Fe Province, Argentina) soils — *Ecologia (B. Aires)*, 0(6): 23–26.

22. Lippert R. D., Hopkins H. H. 1950 – Study of viable seeds in various habitats in mixed prairies – Trans. Kansas Acad. Sci. 53: 355–364.
23. Livingstone R. B., Alessio M. L. 1968 – Buried viable seed in successional field and forest stands, Harvard Forest – Mass. Bull. Torrey bot. Club, 95: 58–69.
24. Major J., Pyott W. T. 1966 – Buried viable seeds in California bunchgrass sites and their bearing on the definition of a flora – Vegetatio, 13: 253–282.
25. Martin A. C., Barkley W. D. 1961 – Seed identification manual – University of California Press, Berkeley–Los Angeles, 221 pp.
26. Naylor R. E. L. 1972 – Aspects of the population dynamics of the weed *Alopecurus myosuroides* Hüds. in winter cereal crops – J. appl. Ecol. 9: 127–139.
27. Numata M., Hayashi K., Komura T., Oki K. 1964 – Ecological studies on the buried-seed population in the soil as related to plant succession. I. – Jap. J. Ecol. 14: 207–215.
28. Olmsted N. W., Curtis J. D. 1947 – Seeds of the forest floor – Ecology, 28: 49–52.
29. Pavone L. V., Reader R. J. 1982 – The dynamics of seed bank size and seed state of *Medicago lupulina* – J. Ecol. 70: 537–548.
30. Pemadasa M. A., Lovell P. H. 1974 – Factors affecting the distribution of annuals in the dune system at Aberffraw, Anglesey – J. Ecol. 62: 379–402.
31. Petrov V. V. 1977 – O zapase žiznesposobnykh semjan v vierchnom sloe počvy pod pologom chwojnogo i melkolistvennogo lesa – Vestn. moskov. Univ., Sek. Biol. 4: 43–56.
32. Petrov V. V., Belaeva I. E. 1981 – State of plant seeds in soil under the forest canopy – Lesovedenie, 5: 44–49.
33. 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.
34. Rabinowitz D. 1981 – Buried viable seeds in a North American tall-grass prairie: the resemblance of their abundance and composition to dispersing seeds – Oikos, 36: 191–195.
35. Rabinowitz D., Rapp J. K. 1980 – Seed rain in a North American tall-grass prairie – J. appl. Ecol. 17: 175–184.
36. Rabotnov T. A. 1954 – Cycle vitale des plantes herbacées vivaces dans les cénooses naturelles – Essais Bot. Acad. Sci. URSS, 2: 137–158.
37. Rabotnov T. A. 1956 – Nekotorye dannye o soderžanii semjan v počve lugovykh soobščestv (In: Akademiku V. N. Sukačevu k 75 letju so dnja roždenija, Ed. V. B. Sočava) – Akad. Nauk SSSR, Moskva – Leningrad, 481–499.
38. Rabotnov T. A. 1960 – Metody opredelenija vozrasta i dlitelnosti žizni u travjanistych rastenij – Polev. Geobot. 2: 249–262.
39. Roberts E. H. 1972 – Dormancy: a factor affecting seed survival in the soil (In: Viability of seeds, Ed. E. H. Roberts) – Chapman and Hall, London, 321–359.
40. Roberts H. A. 1970 – Viable weed seeds in cultivated soils – Rep. natn. Veg. Res. Stn (1969): 25–38.
41. Rysin L. P., Rysina G. P. 1965 – Počvennyj zapas semjan travjanistych rastenij v lesu i faktory vlijajuščie na ich prostranenie (In: Lesa Podmoskovja, Ed. V. N. Sukačev) – Izd. Nauka, Moskva, 5–28.
42. Symonides E. 1978 – Numbers, distribution and specific composition of diaspores in the soils of the plant association Spergulo-Corynephorum – Ekol. pol. 26: 111–122.
43. Symonides E. 1979 – The structure and population dynamics of psammophytes on inland dunes. I. Populations of initial stages – Ekol. pol. 27: 3–47.
44. Symonides E. 1985 – Floristic richness, diversity, dominance and species evenness in old-field successional ecosystems – Ekol. pol. 33: 61–79.
45. Symonides E., Borowiecka M. 1985 – Plant biomass structure in old-field successional ecosystems – Ekol. pol. 33: 81–102.
46. Templeton A. R., Levin D. A. 1979 – Evolutionary consequences of seed pools – Am. Nat. 114: 232–249.

47. Thompson K., Grime J.P. 1979 – Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats – *J. Ecol.* 67: 893–921.
48. Went F.W. 1973 – Competition among plants – *Proc. Natn. Acad. Sci., U.S.A.* 70: 585–590.
49. Yada W.A.S., Tripathi R.S. 1982 – A study on seed population dynamics of 3 weedy species of *Eupatorium* – *Weed Res.* 22: 69–76.
50. Zarzycki K. 1964 – Biological and ecological studies in Carpathian beechwood – *Bull. Acad. pol. Sci. Cl. II, Sér. Sci. biol.* 12: 15–21.

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RECONSTRUCTION OF THE OLD RANGE AND THE PRESENT-DAY BOUNDARY OF A *Potentillo albae-Quercetum* (LIBB) 1933 PHYTOCOENOSIS IN THE BIAŁOWIEŻA PRIMAЕVAL FOREST LANDSCAPE

ABSTRACT: An analysis has been carried out of the ecological and spatial boundaries between deciduous forest communities of the *Potentillo albae-Quercetum* and *Tilio-Carpocetum* types, and the old range has been reconstructed of a selected oak wood in the Białowieża Primaеval Forest. It has been demonstrated that the encroachment of *Carpinus betulus* undergrowth causes thermophilous and heliophilous species to retreat, which leads on to the decline of the oak-wood composition of species at the bioclimate edges and shrinking of the oak-wood area. This process may be the cause of the disappearance of oak-wood sites in north-eastern Poland.

KEYWORDS: *Potentillo albae-Quercetum*, bioclimate boundaries, spatial continuum of vegetation, temporal continuum of vegetation

1. INTRODUCTION

In north-eastern Poland, small-area *Potentillo albae-Quercetum* communities occupy medium-rich, relatively dry habitats usually on table-like tops and southern slopes of moraine and kame hills. In the Białowieża Primaеval Forest, the total area of oak woods shrinks incessantly (Faliński 1968, 1977), but the causes have not so far been established of the decrease in number of sites and bioclimate area, as well as of the relatively low stability of the oak woods. These phenomena can be explained in different ways depending on the accepted concept of their origin.

According to Paerlowski (1930) and Faliński (1968, 1977), Białowieża Forest oak woods are natural climax communities representing relics of a warmer climatic period, whereas directional changes in the dominance structure and species