LONG-TERM CHANGES IN SIZE AND COMPOSITION OF SEED BANK DURING SUCCESSION: FROM MEADOW TO FOREST

KRYSZYNA FALIŃSKA

Polish Academy of Sciences – Institute of Botany
and Białowieża Geobotanical Station, Warsaw University,
PL-17-230 Białowieża, Poland

(Received: April 3, 1998. Accepted: September 21, 1998)

ABSTRACT

Studies of the relation between the size and floristic composition of the seed bank and the vegetation during succession were conducted in the years 1976-1996.

The results of the research did not confirm the hypothesis of directional changes in the density of seeds as the observed changes were of fluctuating nature. At the start of succession the seed bank was small (2970 seeds/m²), and in subsequent years the density of seeds increased successively to reach the highest level after 15 years (9170/m²), then dropped again. After 20 years the density of seeds reached the value recorded at the initial stage (2468/m²). Successional changes in floristic richness of seed bank were directional with the number of species falling from 52 to 24.

All data indicate that the floristic composition of the seed bank is not a mirror reflection of the vegetation structure, but rather a record of a long-term turnover of species and many different events which in various periods of time influenced the inflow of seeds to the soil (spatial dynamics of the necromass, perennial herb and willow canopy structure, seed migration).

KEY WORDS: succession, species composition, soil seed banks, seedlings emergence, abandoned meadow.

INTRODUCTION

The search for succession mechanisms is based on the assumption that the seed bank in the soil is one of such mechanisms (Harper 1977, Cook 1980, Grime 1979, 1981, 1989, Fenner 1987, Leck et al. 1989, Roberts and Vankat 1991, Thompson 1992, van Andel et al. 1993). Hypotheses, according to which in the course of succession the floristic richness of the seed bank decreases and the level of density of seeds in the soil drops during transition from the initial to the terminal stage, have been the subject of most profound interest. So far these hypotheses have been confirmed only in the case of vegetation succession occurring in old-fields (e.g. Numata et al. 1964, Donelan and Thompson 1980, Pickett and McDonnell 1989, Roberts and Vankat 1991). In situations where succession occurred in semi-natural grassland or meadow communities, such direct relationships were not found (Jerling 1983, Thompson 1986, Graham and Hutchings 1988, Milberg 1992, 1995, Milberg and Hansson 1993). Milberg (1995) suggests that results of seed bank studies conducted in chronosequence may be misleading due to the fact that they rarely cover all the stages and are chosen according to varying criteria. Moreover, they are based on different classification systems of vegetation dynamics. All this was indicated in theoretical and methodological discussions on succession studies (Glenn-Lewin and van der Maarel 1992). What is more, simultaneous studies of vegetation dynamics and seed bank conducted in the same place for several years are rare (Williams 1984, Milberg and Hansson 1993). Milberg (1995) who repeated studies on semi-natural grassland after 17-years did

not observe any directional changes in species richness or seed bank size. Significant differences in the evaluation of the size and species composition of the seed bank prompted long-term simultaneous studies of the vegetation dynamics and seed-bank size in an abandoned meadow. They were commenced in the year of meadow abandonment (phase 0) and were scheduled up to the formation of scrub communities, that is to the initial forest phase. It was known from earlier studies that under these conditions the process would last for about 20 years (Falińska 1991). The purpose of the studies was to describe the seed bank pattern for a secondary succession. The objective was to answer the following detailed questions.

Are changes in the floristic composition of the vegetation in abandoned meadows, taking place over a 20-year period, reflected in the species composition of the seed bank, and thus: do the consecutive succession stages show a different seed bank species composition or are the same species present in the seed bank over the whole duration of the process, i.e. from the meadow to the willow scrub stage (early forest phase)?

May species, whose proportion in the vegetation structure is significant, be absent from, or rare in the seed bank during succession; may species, which are rare or absent from the vegetation, constitute a considerable proportion in the seed bank?

The following hypotheses were tested in the present study:

- 1) species richness and diversity decrease during succession;
- 2) seed density (numbers) in the soil decreases during succession;

- 3) the species composition of the seed bank in the initial stage affects the course of succession.

MATERIAL AND METHODS

Study area

The Reski Range is a 15 ha site unforested for 200 years, which is situated in the Narewka River valley close to the Białowieża National Park, in the middle of the Białowieża Primeval Forest (N 52°42'30", E 23°50'20").

The study was conducted between 1976 and 1996 in an abandoned meadow and constitutes a part of a long-term study on demography of successional species, started in 1972 (Falińska 1985, 1991, 1995).

To examine the dynamics of the vegetation of an abandoned meadow, an area of 0.75 ha (50 m x 150 m) within a homogenic *Cirsietum rivularis* patch was marked off, in the year of the cessation of mowing (1976). It was subdivided into 10 m x 10 m (100 m²) squares and properly labelled. Every 5 years changes in floristic composition were assessed in every 100 m² square.

Simultaneously, the seed bank was assessed. For this purpose three plots (A₁, A₂, A₃), 200 m² (2 x 100 m²) large each, were marked off within the study area and subdivided into 5 m x 5 m subplots.

Methods of seed bank estimation

Each of the three plots (200 m² large) was used to study the seed bank by a different method:

(A₁) Seed separation methods. Every 5 years, at the end of the growing season, soil samples were taken. The samples were 100 cm² large and 3 cm thick. Five such samples were taken randomly from 8 subplots (a total of 40) covering an area of 200 m². The soil was transferred to the laboratory where roots and plant remains were removed from it. Subsequently, seeds were picked out with the use of a microscope. In the next step, the seeds were classified and labelled on the basis of a collection of seeds gathered in earlier studies conducted between 1972 and 1980 in the same study area (Falińska 1991). Selected seeds were sown in Petri dishes and seedling emergence was monitored. The data obtained were used for a more precise identification of the species present in the soil.

(A₂) Seedlings emergence from soil samples in greenhouse. In spring – after stratification as in plot A₁, every 5 years 40 soil monoliths, each of 100 cm² (10 cm x 10 cm) in size and 3 cm thick, were taken at random (see A₁). After removing roots and plant remains from it, the soil was placed on laboratory trays at 18–22°C and kept moist with distilled water. Seedling emergence was monitored three times a week for three consecutive years.

(A₃) Seedling emergence in the field. In the year of meadow abandonment, and then every 5 years, ten 1-m² plots were marked off. Every time the plots were located in a different part of the area (200 m²) in order to avoid total destruction of the vegetation. In autumn (October) all plants were removed from the plots. The monitoring of seedling emergence commenced the following year, after disappearance of the snow cover. It was continued till the end of the growing season. The observation was conducted throughout one growing season at 3-day intervals.

Statistical analysis

The density of seeds in the soil was assessed on the basis of the mean number of seeds per 100 cm² calculated from all

samples, and then transformed into the value per m² (by multiplying by 100). Estimates of densities per m² for particular species made use of the mean value per m² and the frequency in the samples (e.g. 20 x mean/100 cm²).

T-tests were used to assess the significance of differences between mean densities of seeds ($\bar{x} \pm SE$) in different phases of succession, while the relationships between the species compositions of the vegetation and the seed bank were assessed using Spearman's rank correlations.

RESULTS

Changes in floristic composition on the abandoned meadow vegetation

Over the 20 years of study the species composition of the meadow community (*Cirsietum rivularis*) changed considerably. Meadow species retreated gradually, although many of them still occurred sporadically in the willow scrub even after 20 years (Table 1). Five years after the abandonment of the meadow macroforbs and sedges formed aggregations. After 10 years macroforbs and willows formed many aggregations which included forest herbs and young trees (*Populus*, *Alnus*, *Betula*). After 15 years swamp species began to play the role of dominant and sub-dominant species, e.g. *Carex acutiformis*, *Carex cespitosa* and willows. After 20 years almost half of the patch of the former meadow (0.75 ha) was occupied by willows, while the remaining part was overgrown with macroforbs and sedges. The following stages were distinguished in the dynamics of the abandoned meadow vegetation:

1. The initial stage (0–5 years) which showed considerable changes of the spatial relations between the meadow species populations.
2. The temporary stage (5–15 years):
 - early phase (5–10 years): the dominance of sedges and macroforbs increased;
 - late phase (10–15 years): willow scrub appeared.
3. The terminal stage (early forest phase 15–20 years): formation of willow brushwood.

Floristic richness of the vegetation and seed bank in the soil

A total of 81 species occurred on the abandoned meadow over the 20 years study. In various periods the number of plant species varied between 41 and 50, and in the seed bank between 52 and 24. As a rule, the species present in the vegetation were present also in the seed bank, though not necessarily at the same time. Twenty species occurred across all the stages of succession in the vegetation and in the seed bank. No seeds of species other than those occurring in the vegetation, even sporadically, during the 20 years, were found in the soil. Generally, the results also demonstrate that the composition of seed bank corresponds to that of the vegetation (Table 1).

Correlations between the species composition of the seed bank and of the vegetation are ever lower in consecutive phases, though still high in absolute terms in phases 0, 1 and 2 (at $r=0.95$; $r=0.79$ and $r=0.65$ respectively). Only in the third and fourth phases do significant differences between the species compositions of the seed bank and the vegetation appear ($r=0.35$; $r=0.28$ respectively).

Seed bank size and species proportions

Over the 20 years the density of seeds in the soils changed significantly (Table 2). The lowest density of seeds in the soil (2468/m²) was found under closed-canopy brushwood and in the initial stage of succession (2970/m²). The highest seed

TABLE 1. Comparison of the floristic composition of the vegetation and seed bank in the soil during succession. * Presence in total seed bank for genera (*Cirsium*, *Viola*, *Carex*, *Salix*) and family (*Poaceae*). Data from the seed separation method

Species	Vegetation						Seed bank				
	after years	0	5	10	15	20	0	5	10	15	20
	phases	0	1	2	3	4	0	1	2	3	4
Meadow species:											
<i>Lychnis flos-cuculi</i>		•	•	•		•	•	•	•	•	•
<i>Ranunculus acris</i>		•	•	•			•	•	•	•	•
<i>Rumex acetosa</i>		•	•	•			•	•	•		
<i>Lathyrus pratensis</i>		•	•	•	•	•	•		•	•	
<i>Viola palustris</i>		•	•	•	•	•	•	•	•		•
<i>Ranunculus repens</i>		•	•	•	•	•	•	•	•	•	•
<i>Caltha palustris</i>		•	•	•		•	•		•	•	
<i>Myosotis scorpioides</i>		•	•				•	•	•		•
<i>Cirsium rivulare</i>		•	•	•	•	•	•	•	•	•	•
<i>Cirsium palustre</i>		•	•	•	•	•					
<i>Geum rivale</i>		•	•	•	•	•	•			•	
<i>Polygonum bistorta</i>		•	•	•	•	•		•	•		•
<i>Potentilla palustris</i>		•	•	•	•	•	•	•			
<i>Trifolium repens</i>		•	•	•			•				
<i>Galium palustre</i>		•	•	•			•	•	•	•	•
<i>Cerastium holsteoides</i>		•	•	•			•	•	•		
<i>Filipendula ulmaria</i>		•	•	•	•	•	•	•	•	•	•
<i>Lythrum salicaria</i>		•	•	•	•	•	•	•	•	•	•
<i>Lysimachia vulgaris</i>		•	•	•	•	•	•	•	•	•	•
<i>Juncus effusus</i>		•	•	•	•	•	•	•	•	•	•
<i>Mentha arvensis</i>		•	•	•	•	•	•	•	•	•	
<i>Epilobium palustre</i>		•	•	•			•		•		•
<i>Galeopsis tetrahit</i>		•	•	•			•		•		
<i>Ranunculus flammula</i>		•	•				•	•			
<i>Lotus corniculatus</i>		•	•				•				
<i>Polemonium caeruleum</i>		•	•				•			•	
<i>Cardamine pratensis</i>		•	•				•	•		•	
<i>Campanula patula</i>		•	•				•			•	
<i>Potentilla anserina</i>		•	•				•	•	•	•	
<i>Plantago lanceolata</i>		•	•				•			•	
<i>Geranium palustre</i>		•	•				•	•	•		
<i>Vicia cracca</i>				•			•		•		
<i>Phragmites australis</i>				•	•	•					
<i>Taraxacum officinale</i>				•			•				
<i>Scirpus sylvaticus</i>				•	•	•	•	•	•	•	
<i>Senecio jacobaea</i>				•	•		•			•	
<i>Viola epipsila</i>				•	•	•					
<i>Crepis paludosa</i>				•	•	•	•				
<i>Symphytum officinale</i>				•	•	•				•	
<i>Urtica dioica</i>				•	•	•	•	•	•	•	•
<i>Valeriana officinalis</i>				•	•	•	•				
<i>Festuca pratensis</i>		•	•	•	•	•					
<i>Poa pratensis</i>		•	•								
<i>Agrostis stolonifera</i>		•	•								
<i>Holcus lanatus</i>		•	•								
<i>Poa palustris</i>		•	•								
<i>Poa trivialis</i>		•	•								
<i>Deschampsia cespitosa</i>		•	•								
<i>Alopecurus pratensis</i>		•	•								
<i>Anthoxanthum odoratum</i>		•	•								
<i>Festuca gigantea</i>		•	•								
<i>Glyceria fluitans</i>		•	•								
<i>Phleum pratense</i>		•	•								
<i>Lolium perenne</i>		•	•								
<i>Agrostis tenuis</i>		•	•								
<i>Dactylis glomerata</i>		•	•								
<i>Phalaris arundinacea</i>		•	•								
<i>Molinia caerulea</i>			•	•	•						
<i>Poaceae</i> (total of seeds)							•	•	•	•	•
<i>Carex flava</i>		•	•								
<i>Carex nigra</i>		•	•								
<i>Carex acutiformis</i>			•	•	•	•					
<i>Carex cespitosa</i>			•	•	•	•					
<i>Carex appropinquata</i>			•	•	•	•					
<i>Carex</i> sp. (total of seeds)							•	•	•	•	•

TABLE 1. Cont.

Species	Vegetation						Seed bank				
	after years	0	5	10	15	20	0	5	10	15	20
	phases	0	1	2	3	4	0	1	2	3	4
Forest herbs:											
<i>Scutellaria galericulata</i>			•	•	•	•		•	•	•	•
<i>Solanum dulcamara</i>				•	•	•					•
<i>Angelica sylvestris</i>				•	•	•					
<i>Peucedanum palustre</i>				•	•	•	•			•	•
<i>Lycopus europaeus</i>				•	•	•			•	•	•
<i>Anemone nemorosa</i>				•	•	•			•	•	
<i>Aegopodium podagraria</i>					•	•		•		•	
<i>Geum urbanum</i>						•					•
<i>Geranium robertianum</i>						•					•
<i>Cardamine amara</i>						•					•
<i>Impatiens noli-tangere</i>						•					•
Woody species:											
<i>Salix cinerea</i>				•	•	•		•	•	•	•
<i>Salix pentandra</i>				•	•	•					
<i>Salix aurita</i>				•	•	•					
<i>Betula pendula</i>					•	•	•			•	•
<i>Frangula alnus</i>					•	•					
<i>Populus tremula</i>					•	•					
<i>Alnus glutinosa</i>					•	•			•		•

Fig. 1. Changes in the contribution (%) of particular species groups to the vegetation and seed bank during succession.

density in the bank was recorded after 15 years at the temporary stage (9170/m²), i.e. at the time when the vegetation was composed of meadow, macroforb and forest species.

The percent contribution of particular groups of species in the seed bank changed significantly during the 20 study years (Fig. 1). The percentage share of species in the structure of the vegetation cover was compared with the pool of seeds in the soil on the basis of identified groups of plants that showed significant differentiation from one another in the succession process. The basic groups in question were of meadow and forest species, as Table 1 shows. However, in the description

of quantitative relationships, a further division was made into grasses, sedges and so-called "other" species (including *Juncus effusus*, *Scirpus sylvaticus* and *Urtica dioica* and thus those whose presence is often associated with disturbance). Macroforbs were also regarded as a separate group, which included species of *Filipendula ulmaria*, *Lysimachia vulgaris* and *Lythrum salicaria*. These are all species whose role in the structure of meadow vegetation increases markedly after cessation of mowing, as they form a macroforb community. This is reflected in both vegetation cover and seed bank (Fig. 1). In the first year following the abandonment of the meadow

Fig. 2. Variable proportion (%) of particular species groups in the seed bank during succession, assessed with 3 methods:

- a) total number of seeds from all samples of soil;
 b) total numbers seedlings emergence on soil monoliths in greenhouse;
 c) total number of seedlings emergence on plots; 0-4 succession phases.

TABLE 2. Comparison of the total number of seeds from all samples of soil and mean density per sample in consecutive phases of succession. Data from seed separation method (n=40)

Stage	Total number of seeds	Mean $\pm$ SE/100 cm ²	Density of seeds per m ²
0	1190	29.75 $\pm$ 3.56 ***	2975
1	3166	79.15 $\pm$ 10.24 NS	7915
2	2755	68.88 $\pm$ 11.16 *	6888
3	3668	91.70 $\pm$ 14.23 ***	9170
4	987	24.68 $\pm$ 4.81	2468

*P<0.05; ***P<0.001; NS – not significant

(Stage 0), seeds of meadow species constituted 64% of the bank, and in the subsequent years their proportion decreased gradually to 17%. At the same time the proportion of forest species seeds increased considerably (from 0.5% to 23%). Significant changes in the floristic composition of the bank occurred at the temporary stage of succession. At that time the so-called "other species", e.g. *Urtica dioica* and *Juncus effusus* constituted 40% of the seed pool, though their proportion in the vegetation increased only slightly (Fig. 2). The remaining part of the seed pool included meadow, macroforb,

grass, sedge and forest species. In the willow scrub that had formed forest species seeds constituted 1/4 of the bank, seeds of the macroforbs species another 1/4, and the other half was made up of various other species.

Relationships between the species composition of the vegetation and the seed bank

A comparison of the floristic composition of the vegetation and seed bank during succession (Table 1; Figs 1, 2) indicates that:

- a gradual decrease in the proportion of meadow species (as a group) in the vegetation was reflected in the seed bank. However, many of the species could be found in the bank up to the initial forest phase (e.g. *Cirsium palustre*, *Lychnis flos-cuculi*, *Ranunculus acris*) even though they were absent or extremely rare in the vegetation at that time;
- the appearance of the forest species in the vegetation and their simultaneous occurrence in the seed bank, were intensified after 15-20 years; seeds of certain forest species occur sporadically at the initial succession stage;
- a significant increase in the proportion of sedges (up to 40%) in the vegetation structure, especially at the temporary stage, was reflected in the seed bank but their proportion in the seeds pool was small (from 5 to 13%; Fig. 2);
- a significant increase of the proportion in seed bank, especially at the temporary stage, of the species such as: *Juncus effusus*, *Scirpus sylvaticus*, *Urtica dioica* (from 6 to 40%) was not reflected in the vegetation structure in which their proportion was small (about 10%).

TABLE 3. Comparison of the total number of seedlings and the mean density per sample in consecutive phases of succession; estimated of the all seedlings emergence in greenhouse (n=40)

Phases	Total number of seedlings	Mean $\pm$ SE/100 cm ²	Density of seedlings per m ²
0	756	18.90 $\pm$ 1.74 ***	1890
1	1621	40.52 $\pm$ 1.81 NS	4052
2	1660	41.50 $\pm$ 2.48 *	4150
3	1033	25.28 $\pm$ 2.87 *	2528
4	498	12.45 $\pm$ 1.81	1245

*P<0.05; ***P<0.001; NS – not significant

Emergence of seedlings in the greenhouse

The number of species making up the bank of germinable seeds (seedling emergence on soil monoliths in greenhouse) ranged from 41 to 26 and was similar to the number obtained as a result of picking seeds out of the soil (52-35).

The lowest density of seedlings (1250/m²) was observed in soil monoliths taken from under the willow scrub (after 20 years) and from the meadow-stage 0 (1890/m²). The highest density was found after 5 years at the initial stage (4052/m²) and temporary stage (4148/m²), i.e. after 10 years (Table 3).

In general, the seed bank size of individual species, assessed with the seedling emergence method was considerably lower than that assessed on the basis of the seeds picked out of the soil (Table 2). However, in both cases a similar regularity of seed density variation in consecutive succession phases was observed, with the lowest density at the early and late stages.

Emergence of seedlings in the plots

During succession seedlings emerging in experimental plots (removal of plants) represented, at different points of time, from 23 to 46 species. The highest number of species (46) in the seedling pool was found 10 years after the cessation of mowing, and the lowest number (23) at the stage 0, i.e. in the first year following the cessation (Table 4). The density of seedlings in the plots varied significantly in the successive years. The lowest density was observed in the meadow at stage 0 (132/m²), and after 20 years in the willow scrub (156/m²). The highest number of seedlings occurred 5 years after the last mowing (432/m²). For 10 years meadow species constituted the largest proportion of the pool of seedlings

TABLE 4. Comparison of the total number of seedlings from all plots and the mean density per m² in consecutive phases of succession (n=10)

Phases	Total number of seedlings	Mean $\pm$ SE/m ²
0	1320	132.00 $\pm$ 21.23 ***
1	4318	431.80 $\pm$ 68.50 NS
2	3470	347.00 $\pm$ 92.33 *
3	2376	237.60 $\pm$ 55.17
4	1568	156.80 $\pm$ 43.12

*P<0.05; ***P<0.001; NS – not significant

(from 92 to 47%). Only after 15-20 years did their proportion drop to 24-16% (Fig. 1). After 5 years the proportion of macroforb seedlings increased, and after 15-20 years forest species constituted 51% of the pool of seedlings. Seedlings of "other species" (*Urtica*, *Juncus*, *Scirpus*) occurred rarely. Their proportion ranged from 2 to 10%. Over the 20 years of study in the experimental plots, seedlings of meadow, grass, macroforb and forest species appeared simultaneously, though in varying proportions (Fig. 1).

In relation to the total bank of seeds in the soil, the density of seedlings in the plots was significantly lower (Table 5). In comparison with the seedlings on the monoliths it was about 10 times lower and in comparison with the total bank – 20-30 times lower. However, the regularity of density variation was similar, i.e. the smallest changes occurred at stage 0 (the meadow) and in willow scrub.

DISCUSSION

Verification of hypotheses

The results of the above described studies do not confirm the hypothesis that the seed density in the soil decreases during succession. In the abandoned meadow, changes in the seed density in the soil were of a fluctuating rather than of directional nature. A low density of seeds in the soil was found at the initial stage of succession (about 3 thousand/m²). The highest density occurred after 15 years (9170/m²) i.e. at the temporary stage. After 20 years the density of seeds was three times lower (about 2.5 thousand/m²), and similar to that recorded at the initial stage. According to earlier studies (Falińska 1981), in a stable (climax) forest community adjacent to the abandoned meadow, the density of seeds was twice as high as in a willow scrub (about 6 thousand/m²).

Neither was such a tendency confirmed by any of the other studies conducted in seminatural communities and on arable land (Graham and Hutchings 1988, Cavers and Benoit 1989, Rice 1989, Levassor et al. 1990, Hester et al. 1991, Milberg 1992). For instance, the highest density of seeds was found at the macroforb stage (Oosting and Humphreys 1940) or as late as in the forest community (Patridge 1989). Directional changes in the density and species richness in the seed bank during succession are described very rarely (Symonides 1986, Pickett and McDonnell 1989, Roberts and Vankat 1991). A tendency of this type is very difficult to explain because numerous vegetation changes taking place in the course of succession are not linear in nature. The floristic composition of the seed bank is determined by the current species composition of communities and depends also upon the vegetation history and the biological properties of plants (Harper 1977, Silvertown 1980, 1981, 1987, Silvertown and Lovett Doust 1993), such as fecundity, seed germination ability (Cook 1980, Fenner 1985, Baskin and Baskin 1989), longevity (Baker 1989, Rice 1989, Milberg 1990, McDonald 1993) migration, mode of seed dispersal (Rabinowitz 1981, Thompson et al. 1993, Hutchings and Booth 1996a, 1996b; etc.). Frequently some of these phenomena can be treated as random events. The fluctuation of seed density in the soil in the course of succession in a meadow, observed in the studies can be explained in the following manner. The lowest number of seeds at the beginning of succession, in spite of the richness of species, results from the fact that the meadows had been mowed in the plant flowering period. As a result, few plants reached their fructification phase. Five years after the last mowing of the meadow the number of seeds was twice as

TABLE 5. Density of seeds in the soil and of seedlings emerging in the experimental plots (A₃) in the meadow at consecutive succession stages. **The highest values at a particular stage are given in boldface**

Species	Number of seeds/m ²					Number of seedlings/m ²					
	after years	0	5	10	15	20	0	5	10	15	20
	phases	0	1	2	3	4	0	1	2	3	4
Meadow forbs:											
<i>Cirsium palustre</i>		320	393	217	144	50	107	74	18	16	5
<i>Lychnis flos-cuculi</i>		200	83	86	16	63	1	32	22	5	5
<i>Ranunculus acris</i>		255	715	996	265	37	26	72	99	27	4
<i>Rumex acetosa</i>		45	45	8			15	15	4		
<i>Lathyrus pratensis</i>		30			3		3	5	8	2	
<i>Lotus corniculatus</i>		60					8	3	2	1	5
<i>Vicia cracca</i>		5		5				15	5		
<i>Cerastium holosteoides</i>		21	10	8				3	1		
<i>Trifolium repens</i>		90					5	45	5		
<i>Polemonium caeruleum</i>		30									
<i>Cardamine pratensis</i>		36	10	8				2	1		
<i>Campanula patula</i>		33						7	5		
<i>Epilobium palustre</i>		40		13		35	7	14	17	13	
<i>Potentilla anserina</i>		50	817	75	30			23	7		
<i>Plantago lanceolata</i>		112			5				9	4	
<i>Polygonum bistorta</i>			68	106		30	6	9	2	2	6
<i>Geum rivale</i>		15			30		3	7	4	10	3
<i>Potentilla palustris</i>		30	367					11	8		
<i>Caltha palustris</i>		140		8	15		10	1	1	1	15
<i>Myosotis scorpioides</i>		80	13	25		82	3	8	3	2	2
<i>Galium palustre</i>		60	104	394	72	34	8	9	14	4	8
<i>Viola sp.</i>		130	281	390		20	5	4	5	4	6
<i>Crepis paludosa</i>		10						6	2	2	3
<i>Symphytum officinale</i>		5			10					4	
<i>Geranium palustre</i>		30	6	45				5	1		
<i>Mentha arvensis</i>		40	13	523	451			12	7	5	
<i>Valeriana officinalis</i>		5									
<i>Filipendula ulmaria</i>		27	86	190	159	81	7	26	67	11	12
<i>Lythrum salicaria</i>		220	927	550	216	78	14	72	54	24	13
<i>Lysimachia vulgaris</i>		60	53	65	17	22		14	20	3	2
<i>Gramineae</i>		263	269	419	40	137	5	13	48	15	1
<i>Carex sp.</i>		140	1172	369	879	36	4	2	16	28	
<i>Taraxacum officinale</i>		5									
<i>Senecio jacobaea</i>		5									
<i>Urtica dioica</i>		27	23	114	752	25		1	4	14	4
<i>Galeopsis tetrahit</i>		5						3			
<i>Juncus effusus</i>		100	858	388	392			84	12		15
<i>Scirpus sylvaticus</i>		25	41	18	43						
Forest forbs:											
<i>Solanum dulcamara</i>											3
<i>Scutellaria galericulata</i>			10	23	73	45		9	8	2	4
<i>Angelica sylvestris</i>										4	2
<i>Peucedanum palustre</i>		10			74	15		1	5	1	1
<i>Lycopus europaeus</i>				239	225	50			3	5	5
<i>Anemone nemorosa</i>				9	3				3	3	1
<i>Aegopodium podagraria</i>			13		8				5	5	4
<i>Geum urbanum</i>						40					
<i>Geranium robertianum</i>						15					
<i>Cardamine amara</i>						69					
<i>Impatiens noli-tangere</i>						90					
Woody species:											
<i>Salix sp.</i>				93	350	88		6	10	110	79
<i>Betula pendula</i>			6		475	70			1	6	12
<i>Frangula alnus</i>							2			1	1
<i>Populus tremula</i>											2
<i>Alnus glutinosa</i>				8		90			4	12	1
<i>Rubus sp.</i>						40					

TABLE 6. Density ($\pm$ SE/100 cm²) variation of the seeds of some species in the soil at the initial, temporary, terminal stages. Density increase >, decrease <, fluctuation $\approx$

Communities Species	Stage	Meadow Initial		Macroforbs Temporary		Brushwood Terminal	Type of changes
<i>Cirsium palustre</i>		4.9 $\pm$ 1.5	NS	8.8 $\pm$ 0.6	*	2.2 $\pm$ 1.5	<
<i>Lychnis flos-cuculi</i>		1.9 $\pm$ 0.6	**	6.8 $\pm$ 1.8	*	1.2 $\pm$ 0.5	$\approx$
<i>Ranunculus acris</i>		8.4 $\pm$ 1.8	NS	6.7 $\pm$ 2.5	NS	4.1 $\pm$ 1.4	<
<i>Filipendula ulmaria</i>		3.2 $\pm$ 1.9	NS	4.5 $\pm$ 2.8	*	2.8 $\pm$ 0.7	$\approx$
<i>Lythrum salicaria</i>		9.6 $\pm$ 3.0	NS	5.0 $\pm$ 1.4	**	3.5 $\pm$ 4.5	<
<i>Lysimachia vulgaris</i>		3.1 $\pm$ 1.9	NS	2.6 $\pm$ 1.3	NS	1.0 $\pm$ 0.0	<
<i>Juncus effusus</i>		18.5 $\pm$ 5.5	NS	28.3 $\pm$ 6.7	**	6.5 $\pm$ 5.5	<
<i>Scirpus sylvaticus</i>		20.7 $\pm$ 2.8	***	1.4 $\pm$ 0.2	**	17.8 $\pm$ 15.0	$\approx$
<i>Urtica dioica</i>		2.2 $\pm$ 3.0	NS	3.4 $\pm$ 1.8	**	4.2 $\pm$ 9.0	>

* – P<0.05; ** – P<0.01; *** – P<0.001; NS – not significant

high. This was the result of on increased supply of seeds to the soil. This, in turn, can be ascribed to the fact that after the cessation of mowing the majority of plants fructify and clonal plants multiply the number of generative ramets. The phenomenon was documented in studies on the demography of species during succession carried out in the same study area (Falińska 1985, 1991). The highest seed density in the soil 15 years after the cessation of mowing resulted from seed accumulation in the soil in the period of abundant fructification of plants and from their limited germination due to the increasing density of clonal plants. The presence in the soil under the canopy of willows of seeds of the meadow species (Table 6) which were no more present in the vegetation indicates that seeds of certain species are long-lived, the fact having been reported also in other studies (Cook 1980, Roberts 1981, Fenner 1985, Milberg 1990, McDonald 1993). It is not quite clear why the seeds of forest species began to appear in the soil so late, i.e. several years after meadow abandonment, in spite of the meadow's adjoining a forest. The study area borders on the Białowieża National Park. It was probably the rich meadow vegetation that was responsible for the limited inflow of migrating seeds to the soil. Seeds may penetrate into the soil only when gaps in the vegetation appear as a result of the death of the clones of the dominating species. This mechanism has been described using the example of *Filipendula ulmaria* clones (Falińska 1995). At the willow scrub formation stage the density of seeds decreased significantly and approached the level recorded for the initial stage of succession.

All the data indicate that as the process of succession progressed the density of forest plant seeds in the soil increased. This has been proved by the results from studies of seed bank in forest communities (Falińska 1981, Pirożnikow 1983, Patridge 1989, Leck et al. 1989, Nakagoshi 1996). It can be presumed that during the return of the forest to the abandoned meadows the seed bank size will grow and decline at least several times, since the process is expected to last about 150-200 years (Faliński 1986).

It is also worth emphasising that apart from facilitating the development of new species compositions which are crucial for the progress of succession, the seed bank also makes the regeneration of the meadow possible in the case the process has been disturbed. This has been proved by the results from the experimental plots. During the 20 years period meadow species constituted a considerable part of the pool of seedlings in these plots, though their proportion decreased gradually in the successive years in favour of the forest species. Moreover, after the removal of the vegetation seedlings developed from the seeds of "other" species were very rare.

Thus, it can be assumed that vegetation removal during succession causes moderate disturbance affecting the preservation of the floristic richness, while elimination of environmental screen still works for foreign species. In the period of 20 years meadow and forest species had better chances to develop than foreign species. That is why it is often assumed that the seed reservoir in the soil is of a great significance for the regeneration of the vegetation following disturbances (Grime 1979, Grubb 1988, Silvertown and Tremlett 1989, Hutchings and Russel 1989, Keddy et al. 1989, Thompson 1992, McDonald 1993, Hutchings and Booth 1996a, 1996b).

Seed bank assessment and the methods used

Recently it has frequently been stressed that possibilities to assess the size and floristic composition of the seed bank are limited by both the biological diversity of seeds and imperfect research methods (Gross 1990). Often, subject to criticism are the size and number of the study plots used. This is due to the fact that researches into temporal variations in floristic composition are conducted in large areas (several hundred square metres large). On the other hand, the seed bank is assessed on the basis of 20-50 soil samples, 10-25 cm² or 50-100 cm² large. Taking into consideration the fact that in heterogeneous vegetation seeds may occur in aggregations (Thompson 1986), and at random (Lavorel and Lebreton 1992) the probability of coming across all the species which make up the seed bank is small. Harper (1977) pointed out that a comparative analysis is very difficult when researches are conducted in two different scales. Another reason, and a very important one, for the low correlation found between the vegetation and the floristic composition of the seed bank is the fact that estimates are usually based on the so called bank of germinable seeds. This means that the size and species composition of the bank is assessed on the basis of the seedlings that emerge from the soil in laboratory conditions. The method is used even though numerous studies (Jensen 1969, Falińska 1981, Hakan et al. 1987) have proved that seeds of certain species do not germinate in laboratory conditions in spite of their high germinating power. Moreover, the germination of seeds in laboratories may spread over 3 years (Falińska 1997) (Table 7), whereas the observation of seedling emergence is carried out only for 3 up to 6 months. Hence, many species may be given no chance to reveal their presence (Johnson 1975).

Estimates of the seed bank size made according to three different methods gave different results. The total number of seeds picked out of the soil was 2-3 times higher than the size of the seed bank assessed with the method of seedling emergence under laboratory conditions, and 10-20 times lower

TABLE 7. Numerical variation of the seedlings which emerged from the seed bank in the laboratory during 3 years. The largest number of seedlings emerged in the second year following the placement of the soil in the laboratory. Data for selected species

Species	Successive year			Total
	1	2	3	
<i>Cirsium palustre</i>	8	77	28	113
<i>Ranunculus acris</i>	7	53	32	92
<i>Rumex acetosa</i>	9	25	2	36
<i>Lathyrus pratensis</i>	7	10	1	18
<i>Geum rivale</i>	1	37	14	52
<i>Myosotis scorpioides</i>	11	55	43	109
<i>Galium palustre</i>	25	73	69	167
<i>Cerastium holosteoides</i>		2	1	3
<i>Urtica dioica</i>		4	4	8
<i>Campanula patula</i>	4	6		10
<i>Polygonum bistorta</i>		5		5
<i>Crepis paludosa</i>		3		3
<i>Lythrum salicaria</i>		4		4

than the value obtained with the method of seedling emergence in experimental plots in the meadow. Of course, one should expect certain differences, if only due to the varying types of seed dormancy, different temperature and humidity requirements (Thompson and Grime 1979, Cook 1980, Grime 1979, Thompson 1987, Fenner 1985, Silvertown 1981, Silvertown and Lovett Doust 1993). The application of a single method does not suffice to determine the full species composition of a seed bank, since a researcher picking out the seeds of the soil may overlook very small seeds, and for many species the short-term observation of seedling emergence in the laboratory may be too short. Jensen (1969) showed that using the seedling emergence method we can distinguish only 40% of the pool of seeds while with the pick out method the proportion ranges from 70 to 80%. Studies of the role of the seed bank in the vegetation dynamics often aim at finding a mirror reflection of the species composition of the vegetation in the seed pool. In such studies the correlation between the species composition of the seed bank and vegetation is assessed at several selected stages (see Milberg 1995). The data obtained are used to describe the nature of seed bank variations during succession. As a result, processes occurring between stages are ignored. These processes can last several or even several tens of years, since stages are distinguished at intervals of such lengths.

Seed bank as a record of the history of changes in the vegetation during succession

In studies of the relations between the floristic composition of the vegetation and the seed bank two possibilities were taken into account:

(a) the seed bank is determined by the species composition of the vegetation, (b) it depends to some extent upon the vegetation composition and in part it reflects numerous other events, including random events. Basically, a significant similarity between the floristic composition of the vegetation and the seed bank was observed in relatively stable forest communities (Johnson 1975, Pirożnikow 1983, Falińska 1981, 1991, Nakagoshi 1996, Jankowska-Balszczuk et al. 1998). Examples of a low correlation between these two elements (Roberts and Vankat 1991, Hakan et al. 1987, Milberg 1992 among others) are more frequent. Most often a weakening of

this correlation is ascribed to disturbances occurring in a community, while its strengthening is associated with the stability of this community (Williams 1984, Patridge 1989).

The study results presented here indicate that in the course of succession in a meadow the latter rather than the former possibility is observed. In successive stages of succession the seed bank contains seeds of species making up the existing vegetation, species which were present in the vegetation of former stages and other species. On the other hand, no significant influence of the initial stage seed bank on the course of succession was observed, contrary to what was suggested by Vankat and Carson (1991). However, meadow species continued to be present in the seed bank up to the formation of the forest community, though many of them retreated from the vegetation much earlier. This fact could indicate a formation of permanent seed banks of meadow species, which was indicated also in other studies (Cook 1980, Fenner 1985, McDonald 1993). Forest species, especially herbs, appeared in the seed bank much earlier than they did in the vegetation. Apparently these were seeds migrating from the forest adjoining the abandoned meadow. A considerable proportion of foreign species in the seed bank, that is species which are not characteristic of meadow or forest communities, was not reflected in the vegetation. Even after the removal of plants from the plots, that is during the experiment simulating a moderate disturbance, the contribution of the species in the vegetation did not increase significantly.

Thus, the floristic composition of the seed bank is not a mirror reflection of the vegetation in successive stages of succession, but rather a record of the history of its changes. This is manifested by the occurrence in the bank of seeds of the species of the preceding, present and future stages of succession and of random events. The nature of the succession process, on the other hand, is revealed by the varying proportions of particular groups of species in the seed bank playing different roles at different stages of the sequence of changes, such as formation of necromass, herb canopy, tree canopy.

Bearing all this in mind one can pose the question: Is there a seed bank pattern typical of succession? From the descriptions of the seed banks presented in various studies one can infer that there are at least three such patterns: (1) a pattern of directional changes, (2) a fluctuation-lottery pattern and (3) a fluctuation pattern.

The first pattern describes unidirectional changes in density and species richness, and hence corresponds with Clement's succession model, i.e. unidirectional changes in vegetation. This type of seed bank was described for cases where succession started in weed community. On the other hand, data from researches conducted in semi-natural meadows indicate that during succession the seed bank rather represents a fluctuation pattern or a fluctuation-lottery pattern which provides a record of a long-term turnover of species and of various processes, significantly affecting the seed bank size and random events.

There are more than one succession models (Glenn-Lewin et al. 1992), so similarly there may be various seed bank models as well (Leck et al. 1989).

Many studies have indicated that succession may follow different paths (Van Der Maarel 1988, Prentice 1986). For instance, at least three such paths were observed in a 15-ha abandoned meadow (Falińska 1991): (1) appearance of trees in the meadow directly without a long-term species turnover, (2) development of patches of 2-3 dominants which after 15 years are colonised by willow and alder trees, (3) the replacement of the floristic compositions according to the classical

Clement's model. The data from the research on the seed bank described in the present paper are representative of the second path of forest return to meadows. The existing data indicate that the course of succession and the seed bank pattern depend on the initial situation, i.e. on the type of vegetation in which succession begins. In environments to a high degree modified by man, where weeds prevail, the pattern of directional changes in species richness and density of seeds in the soil is likely to occur. On the other hand, if succession starts in semi-natural vegetation, the seed bank will rather represent the fluctuation-lottery pattern.

ACKNOWLEDGEMENTS

I would like to thank the anonymous referee for constructive comments on the manuscript.

My special thanks go to the former and present technicians of the Białowieża Geobotanical Station of Warsaw University: Walentyna Maciejewska, Alicja Wiktoruk and Roman Wołkowyczyk, who helped me to collect the material over many years. I am grateful to Halina Kościelecka for typing and preparing the list of references.

This work was partly supported by a grant of the Polish Committee of Scientific Research (KBN).

LITERATURE CITED

- BAKER H.G., 1989. Some aspects of the natural history of seed banks. In: Leck M.A., Parker V.T., Simpson R.L. (eds.). Ecology of soil seed banks. pp. 9-21. Academic Press, San Diego, CA.
- BASKIN J.M., BASKIN C.C., 1989. Physiology of dormancy and germination in relation to seed bank ecology. In: Leck M.A., Parker V.T., Simpson R.L. (eds.). Ecology of soil seed banks. pp. 53-66. Academic Press, San Diego.
- CAVERS P.B., BENOIT D.L., 1989. Seed banks in arable land. In: Leck M.A., Parker V.T., Simpson R.L. (eds.). Ecology of soil seed banks. pp. 309-328. Academic Press, San Diego.
- COOK R., 1980. The biology of seeds in the soil. In: Solbrig O.T. (ed.) Demography and evolution in plant populations. pp. 107-128. Columbia Univ. Press, New York.
- DONELAN M., THOMPSON K., 1980. Distribution of buried viable seeds along a successional series. *Biological Conservation* 17: 297-311.
- FALIŃSKA K., 1981. Experimental investigations of perennial plant populations. *Wiad. Bot.* 25: 209-230.
- FALIŃSKA K., 1985. The demography of coenopopulations of forest herbs. In: White J. (ed.) *The Population Structure of Vegetation*. pp. 241-264. Dr W. Junk Publishers.
- FALIŃSKA K., 1991. Plant demography in vegetation succession. Kluwer Academic Publishers, Dordrecht, Boston, London.
- FALIŃSKA K., 1995. Genet disintegration in *Filipendula ulmaria*: Consequences for population dynamics and vegetation succession. *J. Ecol.* 82: 865-877.
- FALIŃSKA K., 1997. Life history variation in *Cirsium palustre* and its consequences for the population demography in vegetation succession. *Acta Soc. Bot. Pol.* 66: 207-220.
- FALIŃSKI J.B., 1986. Vegetation dynamics in temperate lowland primeval forests. *Geobotany* 8: 1-537. Dr W. Junk Publishers, Dordrecht/Boston/Lancaster.
- FENNER M., 1985. *Seed ecology*. Chapman & Hall, London, New York.
- FENNER M., 1987. Seed characteristics in relation to succession. In: Gray A.J., Crawley M.J., Edwards P.J. (eds.) *Colonisation, succession and stability*. pp. 103-114. Blackwell Scientific Publication, Oxford.
- GLENN-LEWIN D., PEET R.K., VEBLEN T.T., 1992. *Plant succession. Theory and prediction*. Chapman & Hall, London.
- GLENN-LEWIN D.C., VAN DER MAAREL E., 1992. Patterns and processes of vegetation dynamics. In: Glenn-Lewin D.C., Peet R.K., Veblen T.T. (eds.) *Plant succession. Theory and prediction*. pp. 11-59. Chapman & Hall, London.
- GRAHAM D.J., HUTCHINGS M.J., 1988. Estimation of the seed bank of a chalk grassland ley established on former arable land. *J. Appl. Ecol.* 25: 241-252.
- GRIME J.P., 1979. *Plant strategies and vegetation processes*. Chichester, Wiley.
- GRIME J.P., 1981. The role of seed dormancy in vegetation dynamics. *Ann. Appl. Biol.* 98: 555-558.
- GRIME J.P., 1989. Seed banks in ecological perspective. In: Leck A.M., Parker V.T., Simpson R.L., (eds.) *Ecology of soil seed banks*. pp. 15-22. Academic Press, San Diego.
- GROSS K.L., 1990. A comparison of methods for estimating seed numbers in the soil. *J. Ecol.* 78: 1079-1093.
- GRUBB P.J., 1988. The uncoupling of disturbance and recruitment, two kinds of seed bank, and persistence of plant populations as the regional and local scales. *Ann. Zool. Fenn.* 25: 23-36.
- HAKAN S., JONSSON M., OLSEN L.-G., 1987. Buried germinative seeds in mature beech forests with different herbaceous vegetation and soil types. *Holarctic Ecol.* 10: 268-277.
- HARPER J.L., 1977. *Population biology of plants*. Academic Press, London.
- HESTER A.J., GIMINGHAM C.H., MILES J., 1991. Succession from heather moorland to birch woodland. III. Seed availability germination and early growth. *J. Ecol.* 79: 329-344.
- HUTCHINGS M.J., BOOTH K.D., 1996a. Studies on the feasibility of re-creating chalk grassland vegetation on ex-arable land. I. The potential roles of the seed bank and the seed rain. *J. Appl. Ecol.* 33: 1171-1181.
- HUTCHINGS M.J., BOOTH K.D., 1996b. Studies on the feasibility of re-creating chalk grassland vegetation on ex-arable land. II. Germination and early survivorship of seedlings under different management regimes. *J. Appl. Ecol.* 33: 1182-1190.
- HUTCHINGS M.J., RUSSELL P.J., 1989. The seed regeneration dynamics of an emergent salt marsh. *J. Ecol.* 77: 615-637.
- JANKOWSKA-BŁASZCZUK M., KWIATKOWSKA A.J., PANUFNIK D., TANNER E., 1998. The size and diversity of the soil seeds banks and the light requirements of the species in sunny and shady natural communities of the Białowieża Primeval Forest. *Plant Ecology* 136: 105-118.
- JENSEN H.A., 1969. Content of buried seed in arable soil in Denmark and its relation to the weed population. *Dan. Bot. Ark.* 27: 1-55.
- JERLING L., 1983. Composition and viability of the seed bank along a successional gradient on a Baltic sea shore meadow. *Holarctic Ecol.* 6: 150-156.
- JOHNSON E.A., 1975. Buried seed populations in the subarctic forest east of Great Slave Lake, Northwest Territories. *Can. J. Bot.* 53: 2933-2941.
- KEDDY P.A., WISHEN I.C., SHIPLEY B., GAUDET C., 1989. Seed banks and vegetation management for conservation: toward predictive community ecology. In: Leck M.A., Parker V.T., Simpson R.L. (eds.). *Ecology of soil seed banks*. pp. 347-363. Academic Press, San Diego.
- LAVOREL S., LEBRETON J.D., 1992. Evidence for lottery recruitment in Mediterranean old fields. *J. Veg. Sci.* 3: 91-100.
- LECK M.A., PARKER V.T., SIMPSON R.L. eds., 1989. *Ecology of soil seed banks*. Academic Press, San Diego.
- LEVASSOR C., ORTEGA M., PECO B., 1990. Seed bank dynamics of Mediterranean pastures subjected to mechanical disturbance. *J. Veg. Sci.* 1: 339-344.
- MCDONALD A.W., 1993. The role of seedbank and sown seeds in the restoration of an English flood-meadow. *J. Veg. Sci.* 4: 395-400.
- MILBERG P., 1990. What is the maximum longevity of seeds? *Sven. Bot. Tidskr.* 84: 323-352.
- MILBERG P., 1992. Seed bank in a 35 year old experiment with different treatments of a semi-natural grasslands. *Acta Oecol.* 13: 743-752.
- MILBERG P., 1995. Soil seed bank after eighteen years of succession from grassland to forest. *Oikos* 72: 3-13.

- MILBERG P., HANSSON M.L., 1993. Soil seed bank and species turnover in a limestone grassland. *J. Veg. Sci.* 5: 35-42.
- NAKAGOSHI N., 1996. The trend of soil banks in climax forests in Japan. *Verhandlung der Gesellschaft für Ökologie* 25: 301-308.
- NUMATA M., HAYASHI J., KOMURA T., OKI K., 1964. Ecological studies of the buried-seed population in the soil as related to plant succession I. *Jap. J. Ecol.* 14: 207-215.
- OOSTING H.J., HUMPHREYS M.E., 1940. Buried viable seeds in a successional series of old field and forest soils. *Bull. Torr. Bot. Club* 67: 253-273.
- PATRIDGE T.R., 1989. Soil seed banks of secondary vegetation on the Port Hills and Banks Peninsula, Canterbury, New Zealand, and their role in succession. *New Zeal. J. Bot.* 27: 421-435.
- 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*. pp. 123-147. Academic Press, San Diego.
- PIROŻNIKOW E., 1983. Seed bank in the soil of the stabilized ecosystem of a deciduous (*Tilio-Carpinetum*) in the Białowieża National Park. *Ekol. Pol.* 3: 145-172.
- PRENTICE I.C., 1986. Some concepts and objectives of forest dynamics research. In: Fanta J. (ed.) *Forest Dynamics of Western and Central Europe*. pp. 32-41. Pudoc, Wageningen.
- RABINOWITZ D., 1981. Buried viable seed in a North American tall-grass prairie: The resemblance of their abundance and composition to dispersing seeds. *Oikos* 36: 191-195.
- RICE J., 1989. Impacts of seed banks on grassland community structure and population dynamics. In: Leck M.A., Parker V.T., Simpson R.L. (eds.) *Ecology of soil seed banks*. pp. 211-230. Academic Press, San Diego.
- ROBERTS H.A., 1981. Seed banks in soils. *Adv. Appl. Biol.* 6: 1-55.
- ROBERTS T.L., VANKAT J.L., 1991. Floristics of chronosequence corresponding to old field-deciduous forest succession in southwestern Ohio. II. Seed banks. *Bull. Torr. Bot. Club* 118: 377-384.
- SILVERTOWN J.W., 1980. Leaf-canopy-induced seed dormancy in a grassland flora. *New Phytol.* 85: 109-118.
- SILVERTOWN J.W., 1981. Seed size, life span and germination date as co-adapted features of plant life history. *American Naturalist* 118: 860-864.
- SILVERTOWN J.W., 1987. *Introduction to plant population ecology*. Longman Scientific and Technical, Harlow.
- SILVERTOWN J.W., LOVETT DOUST J., 1993. *Introduction to plant population ecology*. Blackwell Science Ltd, Oxford.
- SILVERTOWN J.W., TREMLETT M., 1989. Interactive effects of disturbance and shade upon colonization of grassland: an experiment with *Anthriscus sylvestris* (L.) Hoffm., *Conium maculatum* L., *Daucus carota* L., *Heracleum sphondylium* L. *Functional Ecol.* 3: 229-235.
- SYMONIDES E., 1986. Seed bank in old-field successional ecosystems. *Ekol. Pol.* 34: 3-29.
- THOMPSON K., 1986. Small-scale heterogeneity in the seed bank of an acidic grassland. *J. Ecol.* 74: 733-738.
- THOMPSON K., 1987. Seeds and seed banks. *New Phytol.* 106 (Suppl.): 23-34.
- THOMPSON K., 1992. The Functional Ecology of Seed Banks. In: Fenner M. (ed.) *The Ecology of Regeneration in Plant Communities*. pp. 231-258. C.A.B. International Wallingford, Oxon.
- THOMPSON K., BAND S.R., HODGSON J.G., 1993. Seed size and shape predict persistence in soil. *Functional Ecol.* 7: 236-241.
- THOMPSON K., GRIME J.P., 1979. Seasonal variation in the seed banks of herbaceous species in the contrasting habitats. *J. Ecol.* 67: 893-921.
- VAN ANDEL J., BAKKER J.P., GROOTJANS A.P., 1993. Mechanisms of vegetation succession: a review of concepts and perspectives. *Acta Bot. Neerl.* 42: 413-433.
- VAN DER MAAREL E., 1988. Vegetation dynamics: patterns in time and space. *Vegetatio* 77: 7-19.
- VANKAT J.L., CARSON W.P., 1991. Floristics of a chronosequence corresponding to old-deciduous forest succession in southwestern Ohio. III. Post-disturbance vegetation. *Bull. Torr. Bot. Club* 118: 385-391.
- WILLIAMS E.D., 1984. Changes during 3 years in the size and composition of the seed bank beneath a long-term pasture as influenced by defoliation and fertilizer regime. *J. Appl. Ecol.* 21: 603-615.

DŁUGOTERMINOWE ZMIANY W WIELKOŚCI I KOMPOZYCJI BANKU NASION PODCZAS SUKESJI: OD ŁĄKI DO LASU

STRESZCZENIE

W latach 1976-1996 prowadzono badania nad wielkością i kompozycją gatunkową banku nasion na porzucanych łąkach. Celem badań było poznanie wzorca banku nasion dla wtórnej sukcesji.

Wykazano, że liczebność nasion w glebie podlega fluktuacji. Największe wartości odnotowano w fazach przejściowych sukcesji, a najmniejsze w fazach: początkowej i końcowej. Zmiany bogactwa florystycznego banku nasion przebiegały kierunkowo, a więc: na początku sukcesji było obecnych 52 gatunków, a w fazie zarośli wierzbowych 24. Stwierdzono duże podobieństwo między kompozycją florystyczną roślinności i banku nasion w pierwszych fazach sukcesji, które malało z postępem sukcesji.

Przedyskutowano wiarygodność trzech metod stosowanych w ocenie zapasu nasion w glebie oraz możliwości rozwoju siewek pochodzących z banku nasion w warunkach naturalnych i laboratoryjnych.

SŁOWA KLUCZOWE: sukcesja, kompozycja gatunków, bank nasion w glebie, wschody siewek, porzucone łąki.