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Seed bank pattern and floristic composition of vegetation patches in a meadow abandoned for 20 years

KRYSTYNA FALIŃSKA

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ABSTRACT: The similarity between seed bank and vegetation species composition was analyzed in relation to changes in composition over time and the spatial pattern of the vegetation of a *Cirsium rivularis* meadow abandoned for 20 years. The study was performed between 1996 and 1998, in four patches dominated by *Carex acutiformis, Filipendula ulmaria, Betula pendula* and *Salix cinerea*. The patches developed in periods of 5 to 9 years after abandonment and persisted for the next 15 years even though forest regrew around them. The seed banks of the four patches differed in size and species richness. The highest seed density was noted in the *Betula pendula* (19940/m^2) patch, and the lowest in the *Salix cinerea* patch (8610/m^2). High species diversity was observed in the seed banks of the patches with *Filipendula ulmaria* (*H'* = 3.4) and *Carex acutiformis* (*H'* = 3.0); in the other two it was lower (*H'* = 2.9, *H'* = 2.8). The highest similarity between the floristic compositions of the seed bank and the vegetation was in the patch with *Filipendula ulmaria* (*IS* = 0.80). It was confirmed that the floristic composition of the *Cirsietum rivularis* community plays an essential role in determining the seed bank on the meadow abandoned for 20 years. Seeds of the majority of meadow species were present in the seed bank although these species had not occurred in the vegetation for many years (e.g., *Lychnis flos-cuculi, Ranunculus acris, Cardamine pratensis, Cerastium holosteoides, Campanula patula*). The paper discusses the reliability of seed bank assessment by one of three methods: *(a)* seed separation, *(b)* seedling emergence from soil samples in the greenhouse, and *(c)* seedling emergence in the patches after removal of plants. The most reliable results were obtained when the three methods were used simultaneously. The seed bank pattern of the patchy vegetation of the abandoned meadow was characterized by diversity, heterogeneity, and similarity between the compositions of the seed bank and the vegetation.

KEY WORDS: seed bank pattern, seed longevity, patchiness of vegetation, wet meadow, species composition

K. Falińska. Institute of Botany, Polish Academy of Sciences, and Białowieża Geobotanical Station, Warsaw University, PL–17–230 Białowieża, Poland; e-mail: falinska@tilia.bsg.bialowieza.pl

INTRODUCTION

Seed banks and their relationship to vegetation have been the subject of many recent papers. Many authors report similarities or dissimilarities between the vegetation and the seed bank (see Leck *et al.* 1989).

Similarities between floristic and seed bank composition usually have been established in natural vegetation including, for example, Białowieża Primeval Forest communities (Falińska 1981, 1998; Pirożnikow 1983; Jankowska-Błaszczuk *et al.* 1998). A relatively high similarity between the compositions has been found in communities with domination of annual species (Milberg & Hansson 1993; Morgan 1998) and in rich-meadow communities (Jutila 1998; Peco *et al.* 1998; Falińska 1998, 1999).

Many authors studying grassland predominated by perennial grasses have found low similarities between the seed bank and vegetation (e.g., Douglas 1965; Johnston *et al.* 1969; Roberts 1972; Thompson & Grime 1979; Thompson 1986; Fischer 1987; Milberg 1995; Bakker *et al.* 1996). The lack of correlation between these two compositions is often explained as the result of disturbances (Roberts 1981; Jerling 1983; Wisheu & Keddy 1991; Milberg 1992), although there have been reports on high similarity between them after disturbances (Milberg & Hansson 1993).

The floristic composition of the seed bank is determined partly by the current species composition of communities but it also depends on the vegetation history (Grandin & Rydin 1998) and biological properties of plants (Harper 1977; Silvertown 1981). Factors such as fecundity, seed germination ability (Cook 1980; Fenner 1985; Baskin & Baskin 1989), longevity (Baker 1989; Rice 1989; Milberg 1990; McDonald 1993; Thompson *et al.* 1997), migration, mode of seed dispersal (Rabinowitz 1981), life history (Grime *et al.* 1988), and size and shape of seed (e.g., Thompson *et al.* 1993; Bekker *et al.* 1998a) may be important. Other random factors can play a role.

Many patterns describing seed banks fail to reflect the species composition of the aboveground vegetation (see Leck *et al.* 1989). This is often linked with a failure of the seeds of many species to persist in the seed bank (Thompson 1992) but it may also be due a failure to detect some species present in the seed bank by the particular method used (Gross 1990; Bakker *et al.* 1996; Ter Heerdt *et al.* 1996; Thompson *et al.* 1997).

Low similarity between seed bank and vegetation compositions may also result if the study is on a scale smaller than the spatial pattern of the vegetation. If a large area is studied the compositions analyzed are much more similar than if on a small scale, since the number of species is a function of the area size. On a small scale the seeds of low-frequency species (Lavorell *et al.* 1991) or seeds of clumped buried distribution may not be represented in the soil seed bank (Thompson 1986; Bakker *et al.* 1996).

The influence of the seed bank on the vegetation dynamics depends on the time, composition of seeds in the soil, and seed longevity. Assessment of seed longevity is very difficult and is done by comparing the compositions of the seed bank and the vegetation over the same area at different times. Unfortunately, this kind of study rarely has been performed. Most often the chronosequence method is employed or the same area is studied after a long time, 17 years (Milberg 1995) for example.

This paper reports a study aimed at identifying changes in the relations between the species compositions of the seed bank and the vegetation patches on a wet meadow abandoned for 20 years. This study is part of a long-term investigation of vegetation dynamics carried out in 1971–1998 at the Reski Range (15 ha) in Białowieża National Park (Falińska 1991), and a continuation of a study on seed bank dynamics and the pattern of secondary succession in the same area (Falińska 1998, 1999).

After 20 years the forest has returned to cover 70% of the Reski Range abandoned meadows. The rest of the area is occupied by a mosaic of a few patches dominated by sedges, macroforbs and willow. After abandonment a few species forming a patchy spatial pattern have replaced the earlier fine-grain pattern. Since the floristic composition of the community and the seed bank on the meadow when it was mowed 20 years ago was known, it was possible to examine whether the original composition of the *Cirsietum rivularis* community would be reflected in the seed bank after the change of the compositional and spatial pattern.

The particular aims of the study were *(1)* to determine the seed bank pattern for patchy vegetation, *(2)* to describe the influence of the vegetation mosaic on the size and diversity of the floristic composition of the seed bank, *(3)* to describe the similarities and differences between the compositions of the seed bank and different patches, and *(4)* to assess the seed longevity of some species on the basis of the known dates of their retreat from the vegetation (data from Falińska 1991, 1999).

On the basis of the results of the earlier studies, the following hypotheses were formulated: *(1)* similar initial conditions (homogeneous *Cirsietum rivularis* meadow) and the simultaneity of patch formation should lead to similar seed bank compositions; and *(2)* differentiation of seed bank compositions between patches should be affected by the biological properties of the species that first colonize particular patches after meadow abandonment.

Materials and methods

Study area

The seed bank was studied from 1996 to 1998 at a site within the Reski Range part of a 15 ha area of abandoned meadow land that has been the subject of studies on vegetation dynamics (Falińska 1991). The area is part of the Białowieża National Park (52°42′30″N, 23°50′20″E). The floristically rich meadows of the *Cirsietum rivularis* community occupy fertile and wet habitats which once supported flood-plain forest (*Circaeo-Alnetum*). Prior to abandonment the meadows had not received applications of fertilizer or been grazed, and had been only mown once a year (in June or July), on account of the persistence of floodwater in spring and autumn.

The study was carried out in a 0.6 ha area of the meadow to which forest did not return. Within it, four different types of patches were distinguished, classified according to the dominant species: *Carex acutiformis* (A), *Filipendula ulmaria* (B), *Betula pendula* (C) and *Salix cinerea* (D).

Data collection

Patches A and B were divided into 200 m^2 plots and subdivided into 1 m^2 subplots. In patches C and D under tree canopy, two 10 m by 1 m transects (total 200 m^2) were made over a circular area whose shape was determined by the shape of the group of trees. This study was based on 40 soil samples ($10 \times 10 \times 3$ cm) collected at random from all patches in each of the 200 m^2 plots. From the samples collected for each patch, 10 soil monoliths ($10 \times 10 \times 3$ cm) were selected for observation of seed germination in a greenhouse. The other samples were used to select seeds from the soil.

Presence/absence data for the species in the patch vegetation were recorded in each patch in the course of the growing seasons from April to October 1996 and 1997 at intervals of 10 days. These data served as the basis for assessment of the frequency of occurrence of species in the patches. Simultaneously the percentage cover of species was estimated in the same plots for all patches (200 m^2). Soil samples were collected during the same seasons and from the same plots.

Soil samples were collected during the two growing seasons for seed bank size assessment using two different methods. Field observations indicated recruitment from the soil seed bank in particular patches, after removal of all plants.

Nomenclature follows Mirek *et al.* (1995).

Seed separation methods

Sampling to determine the total seed reserve in the soil of all patches was performed after the end of the 1996 growing season so that seeds could be selected over the winter. Soil samples (surface area 100 cm^2, depth 3 cm) were collected in metal containers in each patch (40 samples). After removal of roots and plant fragments with the aid of special sieves, the soil brought to the laboratory was examined for seeds under a microscope. The seeds were then identified using a collection formed in 1972–1980 as part of earlier work in the same area. Identifications were confirmed by germination of selected seeds in Petri dishes.

Seedling emergence from soil samples in the greenhouse

Greenhouse work was based on 10 soil monoliths ($10 \times 10 \times 3$ cm) taken from each patch in the spring of 1997, following a period of stratification. After removal of roots and plant fragments, the soil was placed in cuvettes in a greenhouse at 18–22^{o}C, with soil moisture maintained using distilled water. In earlier studies on the germination of meadow and forest seeds (Falińska 1981), most seeds germinated at this temperature, close to natural conditions during the growing season. The samples were checked for emerging seedlings 2–3 times a week over 2 consecutive years.

Seedling emergence in the field

Plots (10×1 m^2) established within four patches (October 1996) were used to determine seedling emergence in the field following the removal of all plants. Seedling emergence was monitored at 3-day intervals, from the disappearance of snow cover in the following spring until the end of that growing season (1997).

Statistical analysis

One-way analysis of variance was used to test for difference among the sizes of seed banks of different patches.

Seed density in the soil was assessed on the basis of the mean number of seeds per 100 cm^2 calculated from all samples, multiplied by 100 to obtain the value per m^2. Densities per m^2 for particular species were estimated from the mean value per m^2 and the frequency with which the species occurred in the samples (e.g., $20 \times$ means/100 cm^2).

The significance of differences between mean densities of seeds (mean ± SE) in different patches of vegetation was assessed by Student's *t*-test. Similarity between the species compositions of the seed bank and the vegetation was calculated by Jaccard-Steinhaus's similarity coefficient *IS*. In the formula *IS* = 2c/a+b, **c** was the number of species common to the seed bank and the vegetation in patches, **a** was the number of species in the seed bank, and **b** was the number of species in the vegetation of patches. Spearman rank correlation coefficient, r_S, was calculated using the percent presence of species in soil samples and the percent presence in all plots in the vegetation of patches. The seed bank diversity in each patch was calculated using the Shannon diversity coefficient *H'*.

Results

Species composition of the seed banks

The presence of species in the seed bank was assessed by two methods (seed separation methods; seedling emergence on soil monoliths in greenhouse). A total of 52 taxa occurred in the seed bank. In the four patches the number of taxa ranged from 25 to 40; 18 occurred in all patches and 20 were present in only one patch; of the remaining 14, 7 were found in three patches and the other 7 in two patches (Table 1). The frequency of species in the seed bank was different. In the patches of *Carex acutiformis* (A) and *Filipendula ulmaria* (B) high frequency was noted for *Betula pendula, Filipendula ulmaria*, *Cirsium rivulare*, *C. palustre* and *Carex*. For some of the species, high frequency in the seed bank was observed in only one patch, for example *Urtica dioica* in the patch of *Salix cinerea* (D) (Table 1). The floristic compositions of the seed banks in the four patches differed: the number of taxa was the greatest in the patches of *Filipendula ulmaria* (40) and *Carex acutiformis* (35). The seeds found there represented meadow, forest, and swamp species (*H'* = 3.4 and H' = 3.0). In the patches of *Betula pendula* and *Salix cinerea* the seed banks were composed of fewer species, 29 and 25, respectively (*H'* = 2.9 and *H'* = 2.8; Table 2).

Comparison of the floristic compositions of the patches and their seed banks

Comparison of the floristic compositions of the patches and their seed banks revealed the highest similarity between them in the patch of *Filipendula ulmaria*, where the number of species in common reached 67%, while in the other patches it ranged from 50 to 52%. The

Table 1. Comparison of the floristic compositions of the patches and their seed banks on meadow abandoned for 20 years. Patch dominated by Carex acutiformis (A), *Filipendula ulmaria* (B), *Betula pendula* (C) and *Salix cinerea* (D); M – meadow species, F – forest species, S – swamp species.

Patch type / Taxa		Seed bank				Vegetation			
		A	B	C	D	A	B	C	D
Only in seed bank									
M	*Lychnis flos-cuculi*	•	●	•	•				
F	*Rubus* sp.	•	•	•	•				
M	*Galeopsis tetrahit*	·	•	·	•				
M	*Ranunculus acris*	·	·	·	·				
F	*Carpinus betulus*	·	·						
M	*Hypericum perforatum*		•	•					
M	*Lotus corniculatus*				·				
M	*Cardamine pratensis*				·				
M	*Galium aparine*			·					
M	*Lathyrus pratensis*		·						
M	*Cerastium holosteoides*		·						
M	*Campanula patula*		·						
M	*Geranium palustre*	·							
F	*Alnus glutinosa*	·							
Only in vegetation									
F	*Solanum dulcamara*					·		•	•
S	*Phragmites australis*					·			·
M	*Achillea millefolium*					·	·		
M	*Veronica longifolia*						•		
F	*Aegopodium podagraria*						·		
M	*Symphytum officinale*					·			
M	*Vicia cracca*					·			
M	*Angelica sylvestris*					·			
Both in seed bank and in vegetation in all patches									
S	*Carex acutiformis & C. cespitosa*	●	●	•	•	●	•	•	•
M	*Filipendula ulmaria*	●	●	·	•	•	●	•	•
M	*Cirsium palustre & C. rivulare*	●	●	•	•	•	•	•	·
M	*Viola palustris & V. epipsila*	•	•	•	•	·	·	·	·
M	*Lythrum salicaria*	•	•	•	•	•	•	·	·
M	*Ranunculus repens*	●	●	•	●	•	•	·	•
M	*Geum rivale*	•	·	·	•	•	•	·	·
M	*Galium palustre*	•	●	•	•	•	•	·	•
F	*Urtica dioica*	•	•	•	●	•	·	·	•
M	*Myosotis palustris*	·	·	·	·	•	·	·	•
M	*Gramineae*	●	•	●	•	•	·	•	•
Both in seed bank and in vegetation not always in the same patches									
F	*Betula pendula*	●	●	•	•			●	·
S	*Scirpus sylvaticus*	•	·		•	•	•	·	•
F	*Salix cinerea & S. pentandra*	·	·		·	·	·	·	●
M	*Juncus effusus*	•	•	•		•	•	•	•
M	*Comarum palustre*	•	•	•		·	•	·	
M	*Polygonum bistorta*	·	·	·		•	·		
M	*Taraxacum officinale*	·	·	·			·		
M	*Rumex acetosa*		·	•					
M	*Trifolium repens*		·	·			·		
F	*Peucedanum palustre*	·	·			·			
M	*Lysimachia vulgaris*	·	•						
M	*Epilobium palustre*				·	·	·		
M	*Mentha arvensis*		•			·	·		
M	*Caltha palustris*		·				·		·
F	*Lycopus europaeus*		•			·	·		·
F	*Scutellaria galericulata*	·				·		·	·
M	*Potentilla anserina*			·					·

Table 1. Continued.

Taxa \ Patch type	Seed bank A	Seed bank B	Seed bank C	Seed bank D	Vegetation A	Vegetation B	Vegetation C	Vegetation D
Sporadically								
F *Anemone nemorosa*	·					·		·
M *Senecio jacobaea*	·					·		
M *Valeriana officinalis*	·					·		
M *Sagina procumbens*		·				·		
M *Crepis paludosa*		·						
M *Plantago lanceolata*			·					

Frequency: · < 10%; • 11-30%; ● 31-60%; ⬤ > 60%

coefficient of similarity reflecting the presence of given species in the bank and in the vegetation was the highest in the patch of *Filipendula ulmaria* (IS = 0.80, r_S = 0.51, $P < 0.05$) and *Carex acutiformis* (IS = 0.78; r_S = 0.67, $P < 0.01$), while in the other patches it ranged from IS = 0.56 to IS = 0.59 (Table 2). Comparison of the frequencies of the same species in the seed bank and in the vegetation yielded no correlation only in the patch of *Salix cinerea* (r_S = 0.46, *NS*). The coefficient of similarity for the total seed bank was high at IS = 0.76 (data from all patches; Table 2).

The total number of taxa present in the seed bank and/or the vegetation was 60, of which 14 were found only in the seed bank, 8 only in the vegetation, and 38 in both the seed bank and the vegetation. Among the species present only in the seed bank there were 10 meadow species (e.g., *Lychnis flos-cuculi*, *Ranunculus acris*, *Lathyrus pratensis*, *Campanula patula*, *Lotus corniculatus*) 2 tree species (*Alnus glutinosa* and *Carpinus betulus*), and 2 others (*Rubus* sp. and *Galium aparine*). The species occurring only in the vegetation represented meadow, forest and swamp communities (e.g., *Solanum dulcamara*, *Phragmites australis*, *Vicia cracca*, *Aegopodium podagraria*) (Table 1).

Table 2. Some parameters of seed bank for each patch type on abandoned meadow; * $P < 0.05$; ** $P < 0.01$; NS – not significant. B – seed bank; V – vegetation.

Patch type	Similarity coefficient, *IS*	r_S between B and V	Seed bank diversity, *H’*	Species common to seed bank and vegetation (%)
Carex acutiformis	0.78	0.67** (n = 40)	3.0	50
Filipendula ulmaria	0.80	0.51* (n = 40)	3.4	67
Betula pendula	0.59	0.66** (n = 40)	2.9	52
Salix cinerea	0.56	0.46 NS (n = 40)	2.8	50
Total seed bank (data are from all patches; assessed by two methods)	0.76	0.67	7.8	63

Table 3. Comparison of seed bank size of the different patches on meadow abandoned for 20 year. Statistical differences were tested between patch types (*t*-test). * $P < 0.05$, ** $P < 0.01$; NS – not significant.

a – the total number of seeds from all soil samples (separation method)

Patch type	Total number of seeds	Number of samples	Mean ± SE/100 cm^2	Density of seeds per m^2
Carex acutiformis	4201	30	140.03±89.12	14090
			NS	
Filipendula ulmaria	3421	30	114.03±58.00	11403
			**	
Betula pendula	1994	10	199.40±46.80	19940
			**	
Salix cinerea	861	10	86.10±48.70	8610
Total	10477	80	130.96±67.92	13096

b – the total number of seedling emerging on soil monoliths in greenhouse

Patch type	Total number of seedlings	Number of samples	Mean ± SE/100 cm^2	Density of seedlings per m^2
Carex acutiformis	844	10	84.40±52.99	8440
			NS	
Filipendula ulmaria	1070	10	107.00±68.90	10700
			**	
Betula pendula	2033	10	203.30±42.60	20330
			**	
Salix cinerea	289	10	28.90±24.90	2890
Total	4236	40	105.90±46.50	10590

c – the total number of seedlings emerging in the field

Patch type	Total number of seedlings	Number of samples	Mean ± SE/100 cm^2	Density of seedlings per m^2 (mean ± SE)
Carex acutiformis	1366	10	–	136.60±21.92
				NS
Filipendula ulmaria	1012	10	–	101.20±21.02
				NS
Betula pendula	1173	10	–	117.30±20.32
				NS
Salix cinerea	1247	10	–	124.70±35.37
Total	4798	40	–	119.95±43.12

Seed bank size in the patches

Seed bank size, estimated by the method of seed separation, varied significantly in the four patches studied (Table 3a). The highest density of seeds was found in the patch of *Betula pendula* (19940/m^2) and the lowest in the patch of *Salix cinerea*. Seed densities in the patches of *Filipendula ulmaria* (11403/m^2) and *Carex acutiformis* (14090/m^2) were

Table 4. Comparison of the seed density (mean±SE/100 cm^2) of some species in different patches. * $P < 0.05$; ** $P < 0.01$; NS – not significant; *t* – test.

Species	Patches dominated by:						
	Carex acutiformis		*Filipendula ulmaria*		*Betula pendula*		*Salix cinerea*
Lychnis flos cuculi	5.8± 2.5	NS	5.6± 7.4	*	1.0± 0.0	NS	1.5± 1.5
Ranunculus acris	12.0± 6.0	NS	10.1± 4.4	**	1.2± 0.4	**	3.3± 2.6
Cirsium palustre	8.1± 2.2	NS	5.9± 2.0	**	2.9± 2.0	*	1.6± 0.5
Lythrum salicaria	23.5±16.2	*	13.6± 10.0	**	3.2± 2.1	NS	2.8± 3.6
Filipendula ulmaria	9.5± 5.0	*	21.1± 8.5	**	1.0± 0.0	NS	1.0± 0.0
Betula pendula	9.3± 2.5	NS	15.7± 3.6	NS	27.7± 8.8	*	2.7± 1.2
Urtica dioica	4.0± 9.2	**	17.5±12.3	**	6.0± 0.0	**	44.9±21.2
Carex sp.	40.1±32.8	**	14.7± 1.2	NS	3.0± 2.1	**	8.3± 5.3
Rubus sp.	5.8± 3.9	**	1.4± 1.2	**	3.9± 2.9	**	7.8±13.9
Juncus effusus	9.2± 4.7	**	26.4±22.5	**	163.3± 83.4		

similar. Seed bank size estimated by the method of seedling emergence on monoliths in the greenhouse was smaller than that determined by seed separation; almost twice smaller in the patch of *Carex acutiformis* and almost three times smaller in the patch of *Salix cinerea* (Table 3b). Estimates of seed bank size based on all samples (two methods) from the four patches were significantly higher (14514/m^2). The density of some species in the seed bank varied significantly between the patches (e.g., *Juncus effusus, Urtica dioica, Lythrum salicaria* and *Carex* sp.) (Table 4). The two methods gave different estimates of seed bank size (Table 5). Only 56% of the taxa were detected when it was assessed on basis of seedling emergence on the monoliths in greenhouse, while 84% were detected in the soil seed bank analyzed by the separation method.

Seedling emergence on plots in the field

Estimates of soil seed bank size based on seedling emergence following the removal of plants from plots in patches were significantly (up to 10-fold) lower than those using other methods (Table 3c). The density of seedlings in the patches of *Betula pendula* and *Salix cinerea* was similar (117.3/m^2, 124.7/m^2), but the density of seeds in soil was different: it was highest in the patch of *Betula pendula* (19940/m^2) and lowest in the patch of *Salix cinerea* (8610/m^2). The lowest seedling density appeared in the patch of *Filipendula ulmaria* (101.2/m^2), and the highest in the patch of *Carex acutiformis* (136.6/m^2), so the situation was the opposite to that in the soil seed banks (Table 3a).

A total of 50 taxa occurred on plots after plant removal, including 30 meadow, 17 forest and 3 swamp. The number of species in the four patches ranged from 20 to 43 and was the greatest in the patch of *Betula pendula* (Table 6).

Table 5. Comparison of seed bank of species in different patches, as assessed by two methods: A – seed separation method and B – seedlings emergence from soil samples in the greenhouse. M – meadow species; F – forest species; S – swamp species.

Code	Taxa	Patch type							
		Carex	*Filipendula*	*Betula*	*Salix*	*Carex*	*Filipendula*	*Betula*	*Salix*
		A. Density of seeds per m^2				B. Density of seedlings per m^2			
M	*Lychnis flos cuculi*	307	357	100	30	110	890	50	10
M	*Galium palustre*	80	210	160	30	430	1100	40	30
F	*Rubus* sp.	60	17	270	310	10	10	10	20
F	*Urtica dioica*	27	467	60	4490	2060	90	30	2170
M	*Gramineae*	380	357	740	50	1090	870	1520	90
S	*Carex* sp.	3747	1320	170	2380		80	160	20
M	*Geum rivale*	30	23	70	70	10	10		20
M	*Galeopsis tetrahit*	7	17	10	40		10		20
M	*Filipendula ulmaria*	856	1970		30	30	70	10	
M	*Taraxacum officinale*	77	87	100		10			
M	*Juncus effusus*		40	12110		820	3830	16330	
M	*Myosotis palustris*		13	10		90	90		20
M	*Hypericum perforatum*		53	230			350	970	
M	*Lysimachia vulgaris*	10	1327				20		
M	*Trifolium repens*		40	90				10	
M	*Lythrum salicaria*			80		2350	1510	190	140
M	*Rumex acetosa*			60			50	20	
M	*Campanula patula*		40				350		
M	*Cerastium holosteoides*		33				10		
M	*Lathyrus pratensis*		3				20		
M	*Ranunculus repens*	1157	973	90	230				
F	*Betula pendula*	873	1570	2490	190				
M	*Cirsium rivulare*	780	573	200	140				
M	*Viola palustris*	190	47	540	10				
M	*Comarum palustre*	97	110	2200					
M	*Polygonum bistorta*	27	20	10					
S	*Scirpus sylvaticus*	4593	13		120				
F	*Salix* sp.	3	583		100				
F	*Peucedanum palustre*	3	13						
F	*Carpinus betulus*	5	3						
F	*Anemone nemorosa*	193							
M	*Senecio jacobaea*	173							
M	*Valeriana officinalis*	73							
M	*Geranium palustre*	3							
F	*Alnus glutinosa*	3							
F	*Lycopus europaeus*		427						
M	*Caltha palustris*		373						
M	*Crepis paludosa*		50						
M	*Plantago lanceolata*			100					
M	*Cardamine pratensis*				160				
M	*Epilobium palustre*				35				
M	*Lotus corniculatus*				20				
M	*Ranunculus acris*					770	790	60	160
M	*Cirsium palustre*					30	110	10	30
M	*Viola epipsila*					10	30	20	10
F	*Scutellaria galericulata*					60			
M	*Mentha arvensis*						80		
M	*Sagina procumbens*						10		
M	*Potentilla anserina*							540	
M	*Galium aparine*								10

Table 6. Density of seedlings emergence following the removal plants on the plots in different patches. The highest values at a particular patches are given in boldface. M – meadow species; F – forest species; S – swamp species.

Code	Taxa	Patch type			
		Carex acutiformis	*Filipendula ulmaria*	*Betula pendula*	*Salix cinerea*
		Density of seedlings per m^2; after 20 years			
Present in all patches					
M	*Epilobium palustre*	**615**	112	5	8
M	*Viola palustris & V. epipsila*	105	4	1	10
M	*Myosotis palustris*	88	3	7	20
M	*Galium palustre*	62	188	35	11
M	*Gramineae*	45	67	69	19
M	*Filipendula ulmaria*	42	67	54	49
M	*Lythrum salicaria*	39	53	**98**	221
M	*Cirsium palustre*	22	61	64	51
M	*Ranunculus repens*	22	12	17	9
M	*Lychnis flos-cuculi*	19	34	91	21
S	*Carex cespitosa*	18	6	80	12
M	*Lysimachia vulgaris*	18	14	10	5
F	*Salix cinerea*	12	**250**	33	**789**
M	*Cirsium rivulare*	11	7	22	2
M	*Rumex acetosa*	2	6	4	1
M	*Ranunculus acris*	1	2	12	1
Present in three patches					
M	*Juncus effusus*	**134**	46	5	
M	*Lathyrus pratensis*	43	15	6	
M	*Mentha arvensis*	21	6	8	
F	*Urtica dioica*	18	16	5	
M	*Lotus corniculatus*		4	11	1
Present in two patches					
M	*Polygonum bistorta*	20	4		
M	*Geum rivale*		13	13	
M	*Cardamine pratensis*		3		1
M	*Crepis paludosa*	3		2	
M	*Galeopsis tetrahit*		3	3	
M	*Angelica sylvestris*			2	12
F	*Lycopus europaeus*			2	4
Present in one patch					
M	*Ranunculus flammula*	4			
F	*Scutellaria galericulata*	2			
M	*Comarum palustre*		12		
M	*Vicia cracca*		4		
F	*Betula pendula*			**152**	
M	*Caltha palustris*			60	
S	*Scirpus sylvaticus*			58	
M	*Cerastium holosteoides*			48	
F	*Peucedanum palustre*			32	

(cont.)

Table 6. Continued.

Code	Taxa	Patch type			
		Carex acutiformis	*Filipendula ulmaria*	*Betula pendula*	*Salix cinerea*
		Density of seedlings per m^2; after 20 years			
F	*Alnus glutinosa*			32	
S	*Phragmites australis*			28	
F	*Rubus* sp.			26	
F	*Aegopodium podagraria*			16	
F	*Anemone nemorosa*			12	
F	*Frangula alnus*			12	
F	*Impatiens noli-tangere*			12	
F	*Cardamine amara*			10	
F	*Geranium robertianum*			5	
F	*Populus tremula*			5	
F	*Solanum dulcamara*			4	
F	*Geum urbanum*			2	

Proportions of species in the seed banks

Over half of the seed bank in each patch was made up of seeds of one or two species; these were not always the dominant species in the composition of a given patch or those characterized by high frequency in the seed bank (Table 1). For example, 71% of the seed bank in the patch dominated by *Betula pendula* were seeds of *Juncus effusus*. In the patch dominated by *Salix cinerea*, 58% of the seed bank were seeds of *Urtica dioica*, In the patch dominated by sedge, seeds of *Carex acutiformis* (23%) and *Scirpus sylvaticus* (28%) constituted 51% of the seed bank. Only in the patch of *Filipendula ulmaria*, was the size of the seed bank determined by several species such as *Filipendula* (13%), *Betula* (11%), *Lysimachia* (9%), *Juncus* (9%) and *Carex* (9%) (Table 7).

Analysis of the contributions of particular species in the seed bank of the abandoned meadow, on the basis of the data for all patches collected by two methods (seed separation and seedling emergence in the greenhouse) shows that in the total seed bank the contribution of *Juncus effusus* was almost 23%, *Carex acutiformis* and *C. cespitosa* 12%, *Scirpus sylvaticus* 10%, *Urtica dioica* 7% and *Betula pendula* 7%. Their total contribution was 57%. Of the other 46 taxa the contribution of 20 of them ranged from 1% to 6%, and that of the other 26 was below 1% (Table 7). Estimates of the percent contribution of 3 groups of species to the seed bank on the basis of the data for all patches collected by two methods showed that in the total seed bank the contribution of meadow species was 61%, swamp species 22% and forest species 17% (Table 7).

There were significant differences between patches in the contributions of particular species groups: meadow species ranged from 15% to 92%, swamp species from 1% to 51%, and forest species from 7 to 63%.

Table 7. Contribution (%) of species (A) and particular species groups (B) in the seed bank of different patches. Data are from all soil samples (seed separation method) and seed-ling emergence in the greenhouse. *n* – number of seeds and seedlings in all samples; * < 1%.

Taxa	Patch type									
	Carex		*Filipendula*		*Betula*		*Salix*		Total	
	A. Number of seeds and seedlings									
	n	%	*n*	%	*n*	%	*n*	%	*n*	%
Meadow species										
Ranunculus acris & *R. repens*	424	9	371	8	15	*	39	3	849	6
Gramineae	270	5	194	4	226	6	14	1	704	5
Cirsium palustre & *C. rivulare*	264	5	183	4	21	1	17	1	485	3
Filipendula ulmaria	260	5	598	13	1	*	3	*	862	6
Lythrum salicaria	235	5	151	3	27	1	14	1	427	3
Lychnis flos-cuculi	103	2	196	4	15	*	3	*	317	2
Galium palustre	67	1	173	4	20	*	7	1	267	2
Viola palustris & *V. epipsila*	58	1	17	*	56	1	2	*	133	1
Geum rivale	10	*	8	*	7	*	9	1	34	*
Myosotis palustris	9	*	13	*	1	*	2	*	25	*
Galeopsis tetrahit	2	*	6	*	1	*	6	1	15	*
Juncus effusus	82	2	395	9	**2844**	71			3321	23
Comarum palustre	29	1	33	1	276	7			338	2
Taraxacum officinale	24	*	26	1	10	*			60	*
Polygonum bistorta	8	*	6	*	1	*			15	*
Lysimachia vulgaris	3	*	400	9					403	3
Hypericum perforatum			51	1	120	3			171	1
Trifolium repens			12	*	10	*			22	*
Rumex acetosa			5	*	8	*			13	*
Senecio jacobaea	52	1							52	*
Valeriana officinalis	22	*							22	*
Geranium palustre	1	*							1	*
Caltha palustris			112	3					112	1
Campanula patula			47	1					47	*
Crepis paludosa			15	1					15	*
Cerastium holosteoides			11	*					11	*
Mentha arvensis			8	*					8	*
Lathyrus pratensis			3	*					3	*
Sagina procumbens			1	*					1	*
Plantago lanceolata					10	*			10	*
Epilobium palustre							35	3	35	*
Cardamine pratensis							16	1	16	*
Lotus corniculatus							2	*	2	*
Galium aparine							1	*	1	*
Swamp species										
Carex acutiformis & *C. cespitosa*	**1124**	23	404	9	33	1	240	21	1801	12
Scirpus sylvaticus	**1378**	28	4	*			12	1	1394	10
Forest species										
Betula pendula	262	5	471	11	249	6	19	2	1001	7

(cont.)

Table 7. Continued.

Taxa	Patch type									
	Carex		*Filipendula*		*Betula*		*Salix*		Total	
	A. Number of seeds and seedlings									
	n	%	*n*	%	*n*	%	*n*	%	*n*	%
Urtica dioica	214	4	149	3	9	*	**666**	58	1038	7
Rubus sp.	19	*	18	*	28	1	33	3	98	1
Salix cinerea & S. pentandra			175	4			10	1	185	1
Carpinus betulus	1	*	1	*					2	*
Peucedanum palustre	1	*	4	*					5	*
Scutellaria galericulata	6	*							6	*
Lycopus europaeus			128	3					128	1
Anemone nemorosa			58	1					58	*
Alnus glutinosa			1	*					1	*
Total	4928		4448		3988		1150		14514	

	B. Type of species groups									
Meadow species	1923	39	3035	68	3669	92	170	15	8797	61
Swamp species	2502	51	408	9	33	1	252	22	3195	22
Forest species	503	10	1005	23	286	7	728	63	2522	17
Total	4928	100	4448	100	3988	100	1150	100	14514	100
Unknown seeds	117		43		39		0		199	

Discussion

The results confirm the hypothesis that the floristic composition of *Cirsietum rivularis* meadow played an essential role in the seed bank composition after 20 years of meadow abandonment. After this time, 73% of the seed bank composition were meadow species, the majority of which were absent in the vegetation, such as *Lychnis flos-cuculi, Ranunculus acris, Cardamine pratensis,* and *Hypericum perforatum.* According to other authors (Jensen 1969; Falińska 1999) these species were present in the seed bank at the terminal stage of succession. The role of the seed bank depends on the period over which seeds remain viable in the soil, although this is very difficult to determine. The best assessment of seed longevity in the soil can be obtained from burial experiments (Lunt 1995; Bekker *et al.* 1998b; Thompson *et al.* 1997). Observation of long-term changes in the species composition of the seed bank and vegetation in permanent plots allowed the longevity of the seeds of some species to be assessed during succession (Falińska 1998, 1999). In this study the longevity of seeds in soil was estimated on the basis of a comparison with the results of earlier studies carried out before the cessation of mowing on the same meadow (Falińska 1991). Longevity could be inferred on the basis of the known time of retreat of these species from the vegetation (Falińska 1991, 1999) a few years after cessation of mowing, for example in *Lychnis flos-cuculi, Ranunculus acris, Campanula patula, Ga-*

leopsis tetrahit, *Lotus corniculatus*, *Hypericum perforatum* and *Lathyrus pratensis*. The longevity of seeds of these species has been estimated previously (see Thompson *et al.* 1997). Migration of the seeds of these species from neighboring communities not very probable, as the study area is surrounded by forest communities formed as a result of a secondary succession at the same time that the mosaic vegetation formed. The appearance of seeds of forest species is the result of self-sowing of plants from the neighboring forest, since earlier they had been absent in the meadow seed bank (Falińska 1999). The low density of seeds under the canopy of *Salix* can be explained by the fact that with the growth of the willow the ground level became more shaded. Similar results were obtained by other authors. For example, Davies and Waite (1998) found a negative correlation between the age of the willow and the size of the seed bank. The canopy cover, which can produce deep shading at ground level, may inhibit seedling recruitment (Silvertown 1980; Lunt 1995; Morgan 1998). The high density of the seeds of certain species in the soil is a consequence of the large seed production of these species and their presence in the vegetation on the abandoned meadow for 20 years. Among others, this is the case in *Filipendula ulmaria*, *Lysimachia vulgaris*, *Cirsium rivulare* and *Carex*. The high density of the seeds of *Betula pendula* in the patches in which they dominated may suggest that they came from seed rain and that their seeds were dispersed over a long distance.

The hypothesis that durable seed banks may be a survival strategy typical of heliophilous species assumes that the germination of seeds in the soil is obstructed by a lack of incident light (Pickett & McDonnell 1989), and that it is only when plant cover is disturbed and microhabitat conditions change that exposure and germination take place (Thompson & Grime 1979; Thompson 1992; McDonald 1993). The ecological consequence of this hypothesis is disturbance-dependent emergence of seedlings from the seed bank. Species of such genera as *Epilobium*, *Juncus*, *Trifolium* and *Rubus* are capable of forming durable seed banks in some circumstances (Thompson *et al.* 1997). Their seeds bank were present in the meadow studied 20 years after the cessation of mowing. The viability of *Juncus effusus* seeds has been estimated at several hundred years (Milberg 1990; Milberg & Hansson 1993).

Seed bank floristic composition is apparently both a product of the species composition of the current vegetation and a record of the long-term (20-year) substitution of species in four patches. Other factors including patch structure also influence the accumulation of seed in soil. The current conditions in particular patches, such as the development of canopy cover (*Salix*) or the increased density of ramets of clones (*Filipendula*), which can produce shading at ground level, may be inhibiting seedling recruitment. Vegetative reproduction (long-lived clonal plants) may significantly affect the role of the seed bank in patches, as it leads to the formation of compact vegetation (Eriksson & Fröborg 1996; Mitchell *et al.* 1998; Morgan 1998). Only the appearance of gaps may facilitate the emergence of seedlings and vegetation regeneration (Pakeman & Hay 1996; Hutchings & Booth 1996a–b). After removal of the vegetation cover in the patches, the greatest number of species was represented by seedlings in the *Betula* patch, the same one in which the seed bank was the largest of the four patches studied (Tables 3 & 6). Moreover, in this patch the number of seedlings representing forest species was highest in the gaps. On the plots with the cover removed (10 m in each patch), seedlings of 50 species appeared. The number of species in the patches ranged between 20 and 43 (Table 6). When the total number of seedlings emerging on all plots was analyzed, meadow species remained dominant at 60% (forest species 34%, swamp species 6%). Seedlings of 30 meadow species appeared on the plots in the patches, which indicates the great potential of the seeds of these species to regenerate the meadow community (Table 6).

Analysis of the floristic composition of the seedlings in the four patches confirmed that the seeds of many meadow species had remained viable for a long time, as they had not been present in the vegetation for about 10 years (e.g., *Lychnis flos-cuculi, Lathyrus pratensis, Ranunculus acris*) (Falińska 1991).

Milberg and Hansson (1993) postulated that annual species and those with high turnover in the vegetation (short-lived species) occur at relatively higher frequencies in the seed bank than perennial (low-turnover) species do. This hypothesis has been confirmed in grasslands (Morgan 1998), but not by the present results obtained from wet meadow. High perennial seed density in all the patches suggests that many clonal species formed a large, persistent seed bank (e.g., *Filipendula ulmaria, Lythrum salicaria, Lysimachia vulgaris, Carex* sp.). The seed banks on meadow abandoned for 20 years were composed mainly of perennial herb seeds able to form persistent seed banks. The tendency of perennial species to form longer-lived seed banks has been pointed out by other authors (Roberts 1981; Hopkins & Parker 1984; Peco *et al.* 1998; Falińska 1998, 1999).

The results indicate that the secondary spatial differentiation of vegetation on meadow abandoned for 20 years was reflected in both floristic richness and seed bank size. Undoubtedly the patchy spatial pattern of vegetation favors increasing richness and floristic diversity of the seed bank, because different patches offer the best conditions for different species (Table 4). Each of the patches differed from the others by the presence of a few characteristic species different in each patch, as well as by the different frequencies and densities of the common species. This is the result of the different properties of the dominant species, in particular properties which determine the compactness of vegetation (e.g., *Filipendula*), production of litter and necromass (e.g., *Carex*). These factors affect the germination ability of the seeds in the soil and the inflow of seeds to the soil. Other studies show that the size and floristic composition of the seed bank is determined partly by the current species composition of the communities but also by the vegetation history (Grandin & Rydin 1998) and the biological properties of plants (Harper 1977; Silvertown 1980, 1981).

In each patch one of the factors was dominant and determined the characteristics of the corresponding seed bank. A floristically rich seed bank is not always characterized by high density, and vice versa. For instance, the greatest number of species was represented in the seed bank of the *Filipendula ulmaria* patch, but the density of seeds in this seed bank was lower than in the bank of the *Betula pendula* patch, representing almost half the number of species. Clones of *Filipendula ulmaria* very quickly form a compact cover which limits the inflow of new species to the seed bank and at the same time maintains the seeds of meadow species in the bank (Falińska 1995). Necromass, which occupied 1/3 of the *Carex acutiformis* patch area, played a particular role in the formation of the seed bank in the patch. The seed bank in the soil under the necromass contained mainly representatives of meadow species whose seeds were in the soil before the necromass accumulated. It takes 5 to 10 years to accumulate 15–30 cm of necromass (Falińska 1991).

In each patch a different species determined the size of the seed bank. For example, in the *Betula pendula* patch the contribution of *Juncus effusus* seeds was 71%, and in the *Salix cinerea* patch the contribution of *Urtica dioica* seeds was about 58%. This results in part from the local seed clustering effect (Bakker *et al.* 1996), that is, clumped seeds of *Carex* and *Scirpus* in the patch dominated by sedge and clumped seeds of *Juncus* in the *Betula* patch. Several authors have pointed out the high contribution of *Juncus* to seed banks, and their persistence (Roberts 1981; Fischer 1987; Bekker *et al.* 1998a–b).

In spite of the close proximity of the patches that made up the vegetation mosaic replacing the rich meadow, their seed banks were found to be differ significantly in both species composition and size. Changes in seed bank size over the meadow's 20 years of abandonment were estimated on the basis of a comparison with the results of earlier studies carried out before the cessation of mowing on the same meadow. Seed bank size after 20 years of abandonment (13096/m^2) was found to differ from that of the same meadow (2975/m^2) when it was mown (Falińska 1999). The density of seeds was about 5 times higher than that determined 20 years earlier.

Assessment of the seed bank of the mosaic vegetation was performed on the basis of results of the studies conducted by three methods. Recently it has been stressed frequently that the ability to assess the size and floristic composition of the seed bank is limited by imperfect research methods (Gross 1990; Milberg 1990, 1995; Ter Haardt *et al.* 1996; Thompson *et al.* 1997).

Seed bank size estimates made according to three different methods gave different results (Tables 3, 5). The total number of seeds picked out from the soil was 2–3 times higher than the seed bank size assessed by seedling emergence under laboratory conditions, and 20–100 times higher than that suggested by seedling emergence in experimental plots in the meadow. These differences were to some extent expected, if only because of the variation in types of seed dormancy and temperature and moisture requirements (Thompson & Grime 1979; Cook 1980; Fenner 1985; Thompson 1987). No single method can determine the full species composition of a seed bank, because a researcher picking out seeds from the soil may overlook very small seeds, deeply dormant and non-viable seeds, and the period of observation of seedling emergence in the laboratory may be too short to allow full germination of many species. Our results are consistent with those of Jensen (1969), who showed that seedling emergence distinguished only 40% of the pool of seeds while the pick-out method yielded from 70% to 80%. In these studies only 56% of the taxa were detected on the basis of seedling emergence, and 84% by the separation method (Table 5).

The patchy pattern of vegetation on meadow abandoned 20 years ago was reflected in the different seed bank patterns in particular patches: their species compositions varied greatly and the patches had different seed bank sizes. The frequencies of species in the seed banks differed between patches.

Seed bank patterns were distinguished for each patch type:

(1) For patches dominated by *Carex acutiformis* or *Filipendula ulmaria* the pattern is characterized by high species diversity (*H'* = 3.0, *H'* = 3.4) and similarity (*IS* = 0.78, *IS* = 0.80) between the composition of the seed bank and the vegetation, and a high contribution of meadow species in the seed pool (39% and 68%).

(2) For patches dominated by *Betula pendula* or *Salix cinerea* the pattern is characterized by low species diversity (*H'* = 2.8, *H'* = 2.9) and similarity (*IS* = 0.59; *IS* = 0.56) between the composition of the seed bank and the vegetation, and a high contribution of one species in the seed pool (e.g., *Juncus* or *Urtica*).

Secondary spatial differentiation of the vegetation on the abandoned meadow was reflected in the floristic composition and size of the seed bank: high similarity between the composition of the vegetation and the seed bank (*IS* = 0.76), high diversity and richness of species in the seed bank (*H'* = 7.8), and high density of seeds in the soil ($14514/m^2$).

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