THE REALISED AND POTENTIAL SOIL SEED BANK IN THE *POTENTILLO ALBAE-QUERCETUM* COMMUNITY IN THE BIAŁOWIEŻA PRIMEVAL FOREST

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ABSTRACT

Seedling emergence from soil seed bank was studied during 3 growing seasons 1997-1999 in: 1) 60 plots in 3 parts of the *Potentillo albae-Quercetum* patch: A – with *Carpinus betulus* (hornbeam) present only in the herb layer (canopy cover ca. 50-60%), B – after tree felling, at present with hornbeam dominating the shrub layer (cover >90%), C – invaded by hornbeam 30-40 years ago (cover ca. 90%), and in 2) 60 soil samples from objects A, B, C kept in an unheated glasshouse.

The results suggest that the seed bank realised in natural conditions is poorer in species with high light requirements (the Ellenberg indicator values for light ($L \geq 6$) and their seedlings in comparison with the potential seed bank estimated in glasshouse conditions (field: A – 24; B – 17; C – 7, glasshouse : 44; 38; 32 species / 2 m^2, field: 321; 108; 14, glasshouse: 785; 1205; 177 seedlings / m^2, respectively). Contrarily, more species and seedlings with moderate light demand ($L = 3$-5) appeared in the field plots (field: A – 26; B – 25, glasshouse: 20; 14 species / 2 m^2, field: 1014; 310, glasshouse: 328; 71 seedlings / m^2). The shading by hornbeam negatively influences the size of the seed bank (field: A – 1743; B – 1226; C – 680, glasshouse: 1547; 3274; 459 seedlings / m^2) and its species richness (field: A – 55; B – 48; C – 19, glasshouse: 76; 59; 56 taxa / 2 m^2).

Nomenclature: syntaxa – Matuszkiewicz (1981), taxa – Mirek et al. (1995).

KEY WORDS: soil seed bank, seedlings in woods, seedlings in glasshouse, *Carpinus betulus* invasion.

INTRODUCTION

According to the conception of long-term persistent seed bank this type of a survival strategy is characteristic of pioneer plant species which occupy habitats with random unpredictable changes of environmental conditions (e.g. Harper 1977; Pickett and McDonnell 1989). As regards temperate natural forest communities this strategy is attributed to high light-demanding species that have a chance of growing and developing only in gaps after tree felling (e.g. Collins et al. 1985; Evans and Barkham 1992; Thompson 1992). Forming long-lasting seed bank, regarded as optimal in the harsh environment, is opposed to forming bank of seedlings and juvenile individuals, favoured by natural selection in stable environmental conditions typical of natural forest ecosystems (Harper 1977; Pickett and McDonnell 1989).

First report disagreeing with that dichotomous division of the survival strategies of species living in natural communities appeared in the early eighties (Pirożnikow 1983). It was confirmed by the results of subsequent studies carried out in the communities of the Białowieża Primeval Forest (Falińska 1998, 1999; Jankowska-Błaszczuk et al. 1998). It turned out that in the *Tilio-Carpinetum* forest often regarded as a stable community, moreover, located within the strict reserve of the Białowieża National Park, numerous herb layer species form long-lasting seed bank (Pirożnikow 1983; Jankowska-Błaszczuk et al. 1998).The studies done in other patches of the *Tilio-Carpinetum* and *Potentillo albae-Quercetum* communities in the nineties proved that long-term persistent seed banks are formed not only by pioneer species, but also by the forest ones typical of late-successional stages (Jankowska-Błaszczuk et al. 1998; Panufnik and Kwiatkowska 2000). Seed banks in natural mesotrophic deciduous forests, *Tilio-Carpinetum* and *Potentillo albae-Quercetum*, turned out to be reasonably species-rich (more than 50 species per 2 m^2) and of high density (of the order of a few thousand seedlings per 1 m^2).

The problems connected with soil seed banks may be seen from the evolutionary (the increase in fitness of individuals realising this strategy) or ecological viewpoint (the influence of the size and diversity of seed banks on ecological processes). Many authors focus their attention on the influence of the size and diversity of seed banks on demographic processes and community dynamics (e.g. Hester et al. 1991; McDonald 1993; Milberg 1995; Bakker et al. 1996a; Buckley et al. 1997; Falińska 1998, 1999; Kalamees and Zobel 1998; Leck and Leck 1998; Mitchell et al. 1998). Although lots of studies deal with the role of seed banks in succession of communities, the influence of seed banks on community dynamics is still insufficiently documented. In most cases samples are taken from different patches representing separate successional stages, thus conclusions are drawn from comparative data. Many years' studies on the temporal changes of seed bank, occurring within the same patch, are extremely rare. Studying the process of secondary succession in permanent plots, in a series leading from meadow do shady forest, Falińska (1998, 1999) showed that long-term persistent seed bank is formed by many species of both early- and late-successional stages. By means of three methods (extraction of seeds from the soil, seedling emergence in laboratory conditions and natural environment) the author also showed that an estimate of the seed bank size and its species richness significantly depends on the procedure used. It is worth emphasising that most often the density and species composition of seed bank are estimated by seedling emergence in artificially created conditions, in optimum light and moisture. This procedure has become a broadly accepted methodological standard (e.g. Ter Heerdt et al. 1996; Thompson et al. 1997).

In our opinion each of the methods enables to estimate different ecological parameters connected with seed bank. The size of the whole soil seed pool, regardless viability of diaspores, can be estimated by seed extraction from the soil (Gross 1990). Assuming that all seeds are viable, one can estimate the maximum size of seed bank. Next, seedling emergence in a glasshouse gives information on the contribution of viable seeds able to germinate in unlimited light and moisture, thus on the potential size of seed bank.

In natural environment optimal conditions for germination and further growth of seedlings happen sporadically, though they may be realised in some points within a large area in a longer period. In natural conditions in a given year few viable seeds have an opportunity to germinate, and even fewer survive until seedlings can be identified. The whole number of seedlings emerging during a few seasons in particular ecological conditions informs about the realised size of seed bank. An estimate of this parameter makes it possible to predict the role of seed bank in population dynamics, for instance of rare and endangered species, as well as in regeneration and restitution of communities.

One of the spectacular examples of disappearing natural forest communities is the oak forest, *Potentillo albae-Quercetum*, a habitat for numerous scarce plant species. Owing to many studies having been done in permanent plots for the last decades, the process of species withdrawal and diminishing of the patch area is very well documented (Faliński 1986; Kwiatkowska 1972, 1986, 1993, 1994a, b; Kwiatkowska and Wyszomirski 1988, 1990; Kwiatkowska and Solińska-Górnicka 1993; Kwiatkowska et al. 1997). The hypothetical role of seed bank in reversal of the community decline was indicated by Kwiatkowska and Wyszomirski (1988, 1990), the authors of the experiment of cutting down *Carpinus betulus* individuals and disturbing the herb layer in the area of 0.7 ha within the patch of oak forest densely overgrown by the hornbeam saplings and trees.

The study of the size and diversity of the seed bank in the oak forest done using the method of seedling emergence in glasshouse showed that the seed bank is mainly formed by most typical oak forest species with high light demand (Panufnik and Kwiatkowska 2000).

The aim of this study was:

1) to compare the size and diversity of the potential and realised seed bank in the *Potentillo albae-Quercetum* community,
2) to estimate the influence of the shading by the *Carpinus betulus* saplings and trees on the realised seed bank in the gap after tree felling and in the part of the patch constantly shaded by the hornbeam undergrowth since its invasion,
3) to check whether strongly light-demanding species present in the potential seed bank have a chance to grow in natural environment (in experimental gaps in the herb layer simulating small disturbances due to feeding by deer, bisons or wild boars).

STUDY OBJECT

The study was carried out in 3 parts of the *Potentillo albae-Quercetum* patch (further in the text as objects A, B, C). The patch is located in the Białowieża Primeval Forest (23°31′-24°21(E, 52°29′-52°57(N), in the Landscape Reserve of W. Szafer, in the division 443Cb (earlier 417 and 443Cf) of the Hajnówka forest district. The patch was homogenous as regards the species composition and frequency about 30 years ago. It used to occupy the area of 1 ha. As the best preserved one within this region it has been the object of studies on the species composition (Matuszkiewicz 1955; Faliński 1986), spatial structure and regression of oak forest due to the invasion by *Carpinus betulus* (Kwiatkowska 1972, 1986, 1993, 1994a, b; Kwiatkowska and Wyszomirski 1988, 1990; Kwiatkowska and Solińska-Górnicka 1993; Kwiatkowska et al. 1997). The objects A, B, C were chosen within the permanent of the Białowieża Geobotanical Station (Faliński 1986), in parts of the patch which differed in the average age of hornbeam individuals.

The object A is characterised by tree stand structure typical of the oak forest, dominated by *Quercus robur* with the cover not exceeding 60%. *Carpinus betulus* and *Betula pendula* occur there only sporadically. The forest floor is well lighted up. The poorly developed shrub layer is formed by *Carpinus betulus*, *Picea abies*, *Quercus robur*, *Tilia cordata*, Acer *platanoides*, *Corylus avellana* and *Malus sylvestris*, growing in very low densities. The herbaceous vegetation is lush, multi-layered, more than 1 m high and with the cover of about 90%. Although there are many hornbeam individuals, they are not higher than herbs.

The object B is a part of the patch in which the invasion by hornbeam began about 30-40 years ago. In winter 1979/1980 the hornbeam undergrowth and trees were experimentally cut down (Kwiatkowska and Wyszomirski 1988). The invasion of the gap started again as soon as a second generation of the tree grew above the herb layer. The gap with the hornbeam saplings not higher than herbs had remained for about 10 years. At present, the new hornbeam undergrowth dominates the shrub layer, and a few individuals with the height of 5 m grew into the tree stand. Apart from *Carpinus betulus* there are sporadically *Quercus robur* and *Betula pendula*. The cover (including shrubs) exceeds 90%. Due to the strong shading by hornbeam the herb layer is poorly developed with the cover of about 10%.

The object C is located in a part of the patch in which the hornbeam invasion started about 30 years ago, thus the undergrowth and adults of the tree have directly influenced the herb layer for the last 20 years. Hornbeam individuals dominate today the shrub layer and tree stand in this part. The canopy cover does not exceed 90%. In consequence of long-term shading the herb layer covers only a small part of the surface (about 20%).

METHODS

Seedling emergence in woodland

In early spring 1997, in each of the objects a transect of 2 m × 40 m was led and divided into 20 plots of 2 m × 2 m. Next, in the north-western corner of each plot, 20 subplots of 30 cm × 40 cm were established. To eliminate the competition from adults all above-ground parts of plants were removed. The litter was raked up and the surface layer of the soil was loosened to the depth of about 3 cm. The subplots were subsequently sheltered from possible seed rain by cuboidal boxes covered with a fine transparent plastic net. The observation on seedling emergence in the subplots was conducted from the end of April till the end of October during 3 following seasons: 1997, 1998, 1999. The seedlings were identified at the species level if possible, otherwise at the genus (e.g. *Carex*) or family (Poaceae) levels (Csapody 1968). Every time the seedlings identified and counted were removed together with all new sprouts, and the soil surface was thoroughly loosened.

Seedling emergence in glasshouse

From the same transects, in the south-western corner of each plot, 20 soil samples, with the surface area of 0.1 m^2 and 10 cm deep each, were taken systematically every 2 m. The samples were collected in spring from A_1 horizon after raking up the litter. Next, all vegetative parts of plants were removed from the samples, and the thoroughly mixed soil was put into plastic trays of 30 cm × 40 cm. The trays were placed in the unheated glasshouse of the Białowieża Geobotanical Station. The seedling emergence was observed during 3 consecutive seasons. The samples were regularly watered. As the glasshouse location enabled full light influx, the air temperature inside was higher 5-8°C on cloudy days to 10-12°C on sunny days than outside over the whole growing season. The observation was conducted every 10-14 days at the peak of a season, otherwise every 3 weeks. To avoid light competition seedlings were removed every time, and only few were left to grow higher for easier identification. At the end of each season the soil in the trays was deeply mixed and left dry till spring.

Light demand of species

Species light requirements were determined by means of the Ellenberg indicator values for light – L (Lindacher 1995). Ellenberg accepted the following range of L values: 1 – full shadow, 3 – shadow, 5 – half shadow, 7 – half light, 9 – full light plants. The values: 2, 4, 6, 8 indicate intermediate requirements. In our study we divided species into 3 groups: high light-demanding (L = 6, 7, 8), moderately light-demanding (L = 3, 4, 5) and shade-tolerant ones (species with L = 1, 2 plus those with L = 0 that can grow in different light intensity, thus can tolerate shading as opposed to the species with strong light requirements).

Statistical analysis

The significance of differences between a mean number of species and a mean number of seedlings per 0.1 m^2 in particular objects and both in natural and glasshouse conditions was checked using *t* Student test. The significance of correlation between a mean number of seedlings and the light index L as well as between ranks of species, based on their frequencies in seed bank, was checked using the correlation coefficients of Pearson and Spearman, respectively (Sokal and Rohlf 1995). The similarity between the floristic composition of the potential and realised seed banks was calculated using the coefficient P of Steinhaus: P = 2c / a + b (Kulczyński 1928). Regarding the qualitative similarity: c – the number of species common to the potential and realised seed banks; a, b – the number of species in the realised and potential seed bank, respectively. As regards the quantitative similarity, on the grounds of frequency: c – the sum of the lower of each pair of frequencies compared; a, b – the sum of the frequencies in the seed bank in natural and glasshouse conditions, respectively.

RESULTS

Characteristics of the seed bank realised in woodland

Seed bank in all objects studied is dominated by herbaceous plants. Tree (mainly *Carpinus betulus*) and shrub (*Rubus* spp.) seedlings constitute from ca. 10 to 30% of the total. It should be stressed that 1996 was the year of peak seed production by *C. betulus*, which resulted in its profuse seedling recruitment in each object. The highest (32.2%) contribution of hornbeam seedlings in the object C is caused by the presence of generative individuals of the species within the area and in its neighbourhood. The lowest (4.8%) contribution of hornbeam seedlings in B results from a lack of fruiting adults within the object and its vicinity. The latter object is also distinguished from the other by the highest density of the seedlings of *Urtica dioica* and several times higher the number of *Rubus* spp. seedlings (Table 1). High seedling emergence of both is commonly regarded as typical of habitats after tree felling.

It is worth pointing out that in each of 3 objects more than half the seed bank species are those of low frequency (≤ 20%) and a small number of seedlings (< 25 / 2 m^2). Contrarily, species with high frequency (≥ 80%) usually have high seedling density (> 60 / 2 m^2), (Fig. 1, Table 1). In all 60 plots in 3 objects, 63 taxa were identified. Among them only 3: *Anemone nemorosa*, *Carpinus betulus* and *Viola riviniana* are the most frequent (≥ 90%) in each object and characterised by a high number of seedlings, from ca. 70 to 700 / 2 m^2 (Table 1). Among species with relatively high frequency (≥ 50%) are: *Moehringia trinervia*, *Oxalis acetosella* and *Urtica dioica*. The influence of the hornbeam undergrowth and trees causes a significant decrease in the frequency of common forest species in the seed bank, such as: *Hepatica nobilis*, *Stellaria holostea*, *Veronica chamaedrys* (Table 1). All of the species mentioned occur in a different order in the group of the most frequent and abundant ones in each object. The correlation between species ranks (on the basis of their frequencies) in the objects A, B and C turned out to be statistically insignificant (P > 0.05), which indicates a change of dominance structure in the seed bank as a consequence of the long-term shading by the hornbeam undergrowth.

Although the number of species between particular plots is quite variable, spatially it changes less than the number of seedlings present there. The coefficient of variability (standard deviation / mean) in the first case ranges from 20 to 30%, in the second from 30 to 50%.

Dynamics of seedling emergence in woodland

In objects A and C most seedlings emerged in the first season. In the following two season their number strongly decreased (A: 1740; 1322; 722, B: 937; 1124; 642, C: 685; 533; 258 seedlings / 2 m^2) (Table 2). The number of identified taxa decreased only in object A (A: 41; 39; 29, B: 35; 29; 30, C: 11; 10; 14 species / 2 m^2) (Table 2). The least variable (both between years and objects) was the number of shade-tolerant species

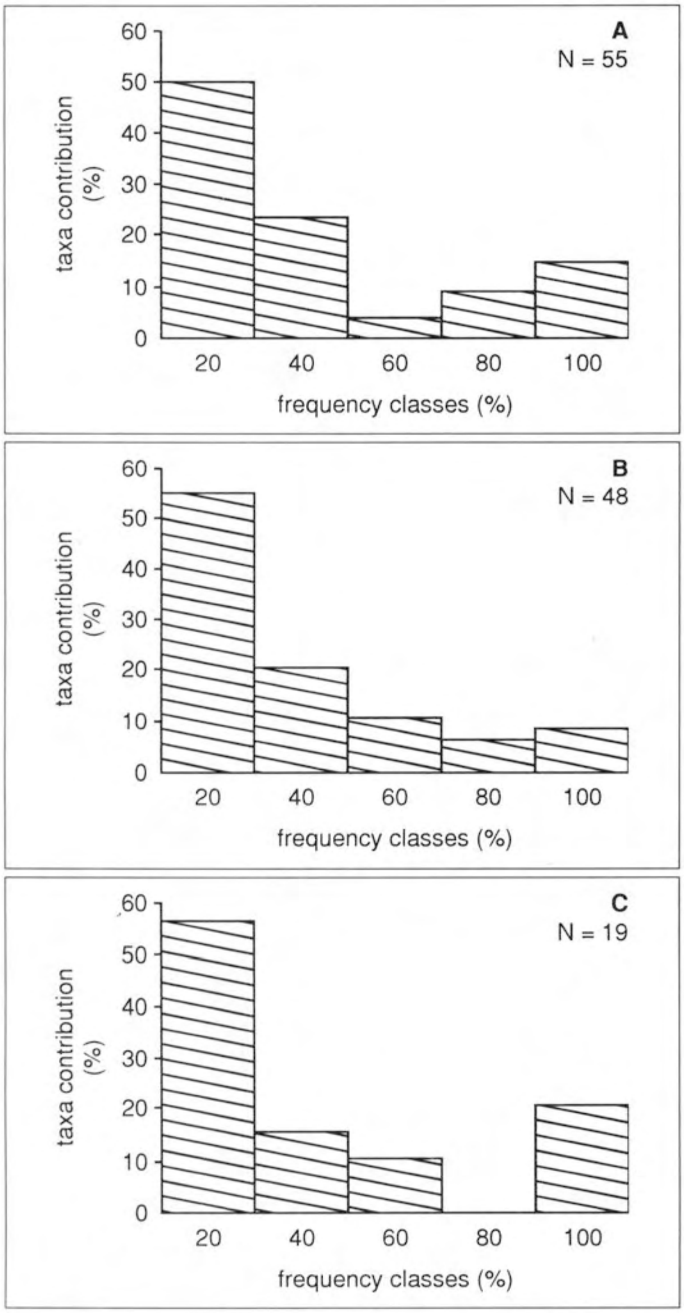

Fig. 1. Frequency of taxa whose seedlings emerged in the plots in 3 parts of oak forest: A – with hornbeam only in the herb layer, B – after tree felling about 20 years ago, at present with dense hornbeam undegrowth, C – invaded by hornbeam 30-40 years ago; 20 plots per an object; N – number of taxa.

(3-5 / 2 m^2). Of the moderately light-demanding species many appeared in the second or both second and third seasons (Table 2). This is why their number in the objects B and C turned out to be the same for both seasons or higher in the third one (second year: 14 and 5, third year: 17 and 5 species / 2 m^2). An analogous result was obtained for strongly light-demanding species in the objects B and C (second: 10 and 2, third: 10 and 6 species / 2 m^2). Considering a mean number of species and seedlings which occurred during 3 consecutive seasons, this tendency becomes much more visible (Table 3). The mean seedling number per 0.1 m^2 of highly light-demanding species is higher in the second and third years in each object (Table 3). Of shade-tolerant species, *Urtica dioica* has its peak recruitment later, which leads to an increase in the mean seedling number of these species during the second season in B (32.3) in comparison with the first one (27.2). As regards moderately light-demanding species the maximum mean seedling density was recorded in the first season (Table 3).

The influence of hornbeam shading on the realised seed bank

The long-term (more than 10 years) shading of the oak forest species with higher light requirements by *C. betulus* present in the shrub layer caused a significant decrease in a number of species and seedlings emerging from the seed bank in the study plots (Fig. 2). In the objects A, B and C the period (t) of the herb layer shading by the hornbeam undergrowth ranges from 0 to 20 years.

In the object A ($t = 0$) there are 18.3 ± 3.6 taxa per 0.1 m^2 on average, in B ($t \approx 10$ years) – 13.9 ± 3.6 and C ($t \approx 20$ years) – only 6.5 ± 1.7 (Table 4). A mean number of seedlings per 0.1 m^2 in A, B, C changes similarly. In all of these cases differences between the objects are statistically significant ($P < 0.01$). In the objects B and C the mean number of moderately light-demanding species ($L = 3$-5) per 0.1 m^2 considerably decreases ($P < 0.01$), which is also the case for their seedlings ($P < 0.001$). Similarly, there is a significant decrease in the mean number of strongly light-demanding species ($L = 6$-8) per 0.1 m^2 ($P < 0.001$) as well as their seedlings ($P < 0.01$). In contrast, the presence of the hornbeam undergrowth did not cause a significant decrease in the seedling density of shade-tolerant species with $L = 0$-2 ($P > 0.1$). Only the mean number of *Urtica dioica* seedlings ($L = 0$) per 0.1 m^2 is significantly higher in the object B ($P < 0.01$). Such a high contribution (about 50%) of *Urtica* to all seedlings is a good indicator of the tree stand disturbance (tree felling) that took place about 20 years ago.

It is worth noticing that seedling emergence in the object B depends on two contrary agents: on the one hand, the 10-year period of suitable light conditions in the experimental gap favourable for seed production and their deposition in the soil, and on the other: much shading due to the renewed spontaneous growth of hornbeam and its recruitment to the shrub layer. The period of the shading by hornbeam is shorter in comparison with C (ca. 10 vs 20 years). At present, light conditions in this object are the worst comparing to the other. The input of new diaspores to the soil after tree felling is strongly evidenced by the increased size of the potential seed bank, estimated in glasshouse conditions, in that the seedling density of moderately and high light-demanding species ($L \geq 3$) reaches 167 per 0.1 m^2 (Table 4). From this potential in natural conditions, beneath the dense canopy of hornbeam almost four times fewer seedlings emerged (46 / 0.1 m^2).

The realised and potential seed bank

Irrespective of the fact that study plots were located in the objects with much light reaching the ground (A) or limited light penetration through the dense hornbeam canopy (B, C), the seed bank realised during 3 consecutive seasons is characterised by a bimodal pattern of species light demand (Fig. 3a). Species with high light requirements ($L = 6$-8) constitute about 30-40% of all seedlings emerged in the plots. The most numerous in this group are the 'half light species' ($L = 7$). The second peak is made by moderately light-demanding ones ($L = 3$-5) with maximum for species with $L = 4$. Contrarily, the species richness of the potential seed bank, estimated in glasshouse conditions, is higher than in the plots, and a pattern of species light demand is unimodal with maximum for species with $L = 7$ (Fig. 3a). Generally, in unlimited light and moisture conditions high light-demanding

TABLE 1. Light demand of species (the Ellenberg light index L), frequency of seedling taxa and a sum of seedlings emerging during 1997-1999 in 20 forest plots in each of the objects A, B, C (description of objects – Fig. 1).

Taxon	Light index L	Frequency (%)			Number of seedlings		
		A	B	C	A	B	C
Genista tinctoria	8	5	5		1	3	
Hypericum maculatum	8		10		1	3	
Trifolium repens	8	5	10	5	1	5	1
Angelica sylvestris	7		5			1	
Betula pendula	7	35			16		
Clinopodium vulgare	7	95	20		173	8	
Fallopia convolvulus	7	5			1		
Fragaria vesca	7	15	5		5	5	
Galeopsis bifida	7	30	20	30	13	6	7
Hypericum perforatum	7	15	25	5	4	26	2
Lathyrus pratensis	7		5			1	
Origanum vulgare	7	10		5	2		1
Primula veris	7	45			30		
Quercus robur	7	5		5	1		1
Ranunculus acris	7		5			2	
Rubus idaeus	7		35			45	
Serratula tinctoria	7	10			2		
Vicia cracca	7	25	20		6	5	
Vicia sylvatica	7	5	10		1	2	
Ajuga reptans	6	25	10		7	3	
Astragalus glycyphyllos	6	10			2		
Calamagrostis arundinacea	6	15	5		10	1	
Campanula rapunculoides	6	10			4		
Galium boreale	6	25			21		
Gnaphalium sylvaticum	6			5			1
Potentilla alba	6	5			2		
Ranunculus polyanthemos	6	5			1		
Stellaria media	6	5			1		
Torilis japonica	6	30	25		12	12	
Veronica chamaedrys	6	85	50	25	307	87	14
Campanula persicifolia	5	10			5		
Convallaria majalis	5	35	10		16	2	
Galium schultessi	5	65	5		116	3	
Hypericum montanum	5	5	5		1	2	
Lapsana communis	5	50	35		82	14	
Lathyrus niger	5	5	10		1	2	
Melampyrum nemorosum	5	85	30		167	20	
Melittis melissophyllum	5	15	10	5	4	5	1
Stellaria holostea	5	100	70	10	148	155	22
Thalictrum aquilegiifolium	5	15			6		
Tilia cordata	5		5			1	
Trientalis europaea	5	15	25		3	10	
Acer platanoides	4	15	5		3	1	
Carpinus betulus	4	100	100	100	713	129	474
Epilobium montanum	4	35	35	10	16	11	2
Geum urbanum	4	20	15		15	8	
Hepatica nobilis	4	80	60	30	154	31	15
Lathyrus vernus	4	35	25		11	5	
Milium effusum	4	10	5		3	1	
Moehringia trinervia	4	80	80	50	187	63	34
Mycelis muralis	4	35			11		
Rubus saxatilis	4	40	65		10	60	
Scrophularia nodosa	4		5		1	1	
Viola riviniana	4	100	100	90	311	128	68
Asarum europaeum	3	20	50		13	18	
Maianthemum bifolium	3	15	15		18	6	
Paris quadrifolia	3		10			2	
Ranunculus lanuginosus	3	35	45	20	13	18	4
Galium odoratum	2		5	5		2	4
Oxalis acetosella	1	75	45	90	102	19	89
Anemone nemorosa	0	100	100	100	522	512	404
Urtica dioica	0	70	100	60	133	989	214
Vicia sepium	0	40	25		15	6	
Galium sp.			15			3	
Sonchus sp.		5			1		
Poaceae		85	35	5	60	17	1
not identified		85	90	55	299	244	117
Total number of seedlings					3784	2703	1476

TABLE 2. Species with maximum seedling recruitment during the second (II) and third (III) season in the forest plots in objects A, B, C (description of objects – Fig. 1).

Taxon		Number of seedlings								
	L	A			B			C		
		I	II	III	I	II	III	I	II	III
Clinopodium vulgare	*7*	21	49	103	2	5	1			
Hypericum perforatum	*7*	2	2		1	22	3			2
Primula veris	*7*	4	15	11						
Rubus idaeus	*7*				2	26	17			
Galium boreale	*6*	7	14							
Melampyrum nemorosum	*5*	9	139	19	9	8	3			
Epilobium montanum	*4*	2	14	10		1	10			2
Geum urbanum	*4*	1	14		1	7				
Hepatica nobilis	*4*	12	38	104	4	11	16		6	9
Moehringia trinervia	*4*	10	120	57	5	45	13		21	13
Rubus saxatilis	*4*	3	5	2		33	27			
Viola riviniana	*4*	23	229	57	7	104	17	4	37	27
Asarum europaeum	*3*	2	6	5	1	16	1			
Maianthemum bifolium	*3*		10	8	3	3				
Ranunculus lanuginosus	*3*	3	7	3	1	7	10			
Oxalis acetosella	*1*	18	36	48	2	8	9	4	53	32
Urtica dioica	*0*	27	56	50	40	619	330	2	184	28

TABLE 3. Characteristics (mean and standard deviation) of the seedling emergence of shade-tolerant (L = 0-2), moderately (L = 3-5) and high (L = 6-8) light-demanding species in 3 seasons 1997-1999 (description of objects – Fig. 1).

	I season			II season			III season		
	A	B	C	A	B	C	A	B	C
Mean number of species with light demand:									
L = 0, 1, 2	2.1 ± 0.8	2.1 ± 0.6	1.1 ± 0.8	2.1 ± 0.9	1.7 ± 0.8	2.1 ± 0.7	1.1 ± 0.6	1.2 ± 0.5	1.6 ± 0.9
L = 3, 4, 5	5.8 ± 1.8	3.3 ± 2.0	1.4 ± 0.7	7.2 ± 1.6	4.4 ± 1.7	2.4 ± 1.0	4.8 ± 1.7	3.7 ± 1.5	1.8 ± 0.8
L = 6, 7, 8	2.7 ± 2.1	1.0 ± 1.1	0.2 ± 0.4	3.0 ± 1.3	1.7 ± 1.4	0.4 ± 0.5	2.6 ± 1.4	1.0 ± 1.2	0.4 ± 0.8
Mean number of identified taxa	10.6 ± 3.4	6.5 ± 2.7	2.6 ± 1.1	12.3 ± 2.9	7.9 ± 2.9	4.9 ± 1.4	8.4 ± 2.1	5.9 ± 2.1	3.8 ± 1.6
Mean seedling number of species with light demand:									
L = 0, 1, 2	23.7 ± 8.6	27.2 ± 12.3	15.4 ± 13.1	9.7 ± 9.9	32.3 ± 35.0	16.6 ± 27.3	5.3 ± 5.8	17.0 ± 19.4	3.6 ± 4.4
L = 3, 4, 5	47.0 ± 15.2	15.2 ± 11.3	18.7 ± 13.3	37.3 ± 18.9	13.2 ± 7.6	8.6 ± 7.2	17.2 ± 10.7	6.4 ± 3.3	3.7 ± 3.2
L = 6, 7, 8	9.5 ± 10.8	1.7 ± 2.7	0.2 ± 0.4	11.0 ± 8.3	6.9 ± 13.8	0.8 ± 1.1	10.8 ± 9.6	2.2 ± 3.7	0.5 ± 1.0
Mean number of identified seedlins	80.5 ± 21.1	44.0 ± 17.1	34.3 ± 22.8	60.2 ± 21.1	53.4 ± 39.1	25.9 ± 29.3	33.6 ± 18.0	25.6 ± 21.0	7.8 ± 5.0

species constitute from 50% (C) to 60% (A) of all of the seedlings emerging in the soil samples. The difference in the range of light requirements of species, whose seedlings emerged in the plots and soil samples, is even more pronounced while comparing a number of seedlings in the realised and potential seed bank. The curves describing patterns of species light demand for a seedling number have different maxima (Fig. 3b). In the forest, most identified seedlings i.e. from about 50 to 60% (except *Urtica dioica*) belong to moderately light-demanding species (L = 3-5), and the seedlings of those with high light requirements (L = 6-8) constitute only 15-20%. In the glasshouse, the seedlings of high light demanders dominate the seed bank with their 40-60% of the total recruitment, whereas the contribution of moderately light-demanding seedlings in 3 objects does not exceed 25%. As a consequence, the similarity of species composition, expressed by the coefficient of Steinhaus in the series of plots and soil samples within the same objects is relatively low (about 40-60%). The values of P based on floristic composition amount: A – 59.5; B – 54.2; C – 40.0%, and based on species frequency: 49.2; 53.6; 42.3%, respectively.

During 3 seasons, in all plots of the series A, 55 taxa per 2 m^2 were recorded (in the glasshouse – 76 / 2 m^2), in B – 48 (59), C – 19 (56). The sum of identified seedlings that emerged during the same period in the plots in the object A amounted 3485 / 2 m^2. For comparison, in the series of soil samples in the glasshouse 3093 seedlings emerged / 2 m^2. In the plots in B, the number of seedlings per 2 m^2 was 2459 (in the glasshouse – 6547) and in C – 1359 (918).

The mean number of identified taxa, whose seedlings emerged in the soil samples, is in all objects significantly higher ($P < 0.01$) than in the analogous series of plots in the forest (Table 4). The increased mean value is mainly caused by the increased number of high light-demanding species, for that light and moisture conditions in the glasshouse turned out to be optimal. In the soil samples from the objects A, B and C there were 44, 38 and 32 species with L = 6-8 per 2 m^2, whereas their num-

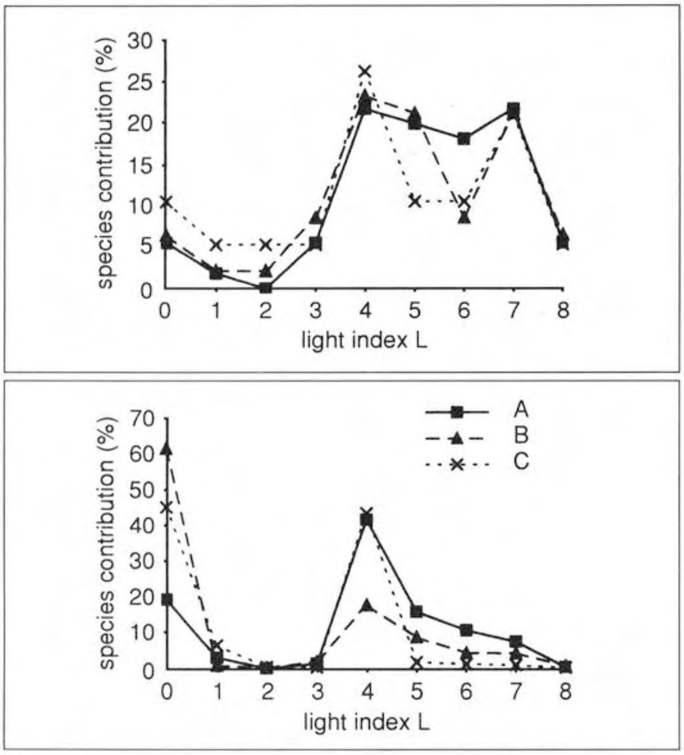

Fig. 2. The period (t) of the herb layer shading by hornbeam and the contribution (%) of species with different light demand (upper figure) and of their seedlings (lower figure) to the total recruitment in the plots in the objects: A (t = 0), B (t ≈ 10), C (t ≈ 20 years); (description of objects – Fig. 1).

bers in the plots were: 24, 17 and 7, respectively. The mean densities of high light-demanding species and their seedlings per 0.1 m^2 in the glasshouse are significantly higher ($P < 0.001$) than in the natural environment in each object (Table 4).

The experimental gaps in the herb layer are favourable for growth of the seedlings of forest species with lower light requirements ($L = 3\text{-}5$). In natural conditions there were more moderately light-demanding species (A: 26; B: 25 / 2 m^2) than in the glasshouse (A: 20; B: 14 / 2 m^2). Their mean number per 0.1 m^2 in the plots in A and B turned out to be almost twice as high ($P < 0.001$). Only in the plots of the series C a little fewer species appeared than in the glasshouse (8 vs 12 / 2 m^2), though the mean number was almost identical. Similarly, significantly more seedlings of moderately light-demanding species emerged in the plots than in the soil samples in the objects A and C ($P < 0.001$). An analogous result was obtained for the seedlings of shade-tolerant species ($L = 0\text{-}2$) in A and C ($P < 0.01$). Only in the object B the mean seedling number of species with $L \leq 5$ was higher in the glasshouse in comparison with the plots, though the difference was insignificant ($P > 0.05$). The visibly higher seedling number of shade-tolerant species in the soil samples from B was mainly caused by profuse emergence of *Urtica dioica*. The potential size of the seed bank of this species turned out to be more than twice bigger (ca. 130 seedlings / 0.1 m^2) in comparison with that in the plots (ca. 50 / 0.1 m^2), which can be seen in the higher mean seedling number of species with $L \leq 2$ (Table 4).

It was stated that the correlation between species light demand and a mean number of their seedlings emerging from the seed bank in given conditions is statistically significant. In unlimited light and moisture conditions, in the glasshouse, the correlation coefficient of Pearson, calculated for 60 soil samples from 3 objects, amounts: $r_p = 0.75$ ($r_p^2 = 0.5625$), for the plots in the forest: $r_p = -0.65$ ($r_p^2 = 0.4225$).

DISCUSSION

The seed bank – potential and realised in natural conditions

In most studies of soil seed banks data on density and species richness are based on the method of seedling emergence in glasshouse or laboratory conditions. According to Thompson et al. (1997) these works constitute about 70% of all published since the beginning of the 20th century, whereas those using the method of seedling recruitment in the field – merely 1%. Among those few ones are: Bakker et al. (1996a), Edwards and Crawley (1999), Falińska (1999).

The probable reason for that many plant ecologists neglect the latter method is that results obtained during one season due to variable weather conditions may be entirely random, where-

TABLE 4. Characteristics (mean and standard deviation) of the realised (plots in forest) and potential (soil samples in glasshouse) seed bank in objects A, B, C during 1997-1999; P_p – the probability of no difference in means between forest plots in 3 objects, $P_{p\text{-}s}$ – between forest plots and soil samples in each object (t Student test); asterisk – difference significant.

	Plots in forest				Samples in glasshouse			
	A	B	C	P_p	A	B	C	$P_{p\text{-}s}$
Mean number of species with light demand:								
L = 0, 1, 2	2.9 ± 0.7	2.8 ± 0.7	2.6 ± 0.7	> *0.95*	2.1 ± 1.1	2.3 ± 0.9	2.8 ± 1.0	> *0.95*
L = 3, 4, 5	10.2 ± 2.1*	8.2 ± 2.4*	3.2 ± 1.1*	< *0.01*	5.9 ± 1.9*	5.4 ± 1.7*	3.3 ± 1.6	< *0.001*
L = 6, 7, 8	5.2 ± 2.2*	2.7 ± 1.6*	0.8 ± 0.8*	< *0.001*	12.5 ± 3.1*	11.6 ± 2.8*	6.4 ± 2.0*	< *0.001*
Mean number of identified taxa	18.3 ± 3.6*	13.9 ± 3.6*	6.5 ± 1.7*	< *0.01*	22.8 ± 4.9*	20.3 ± 4.2*	13.8 ± 3.0*	< *0.01*
Mean seedling number of species with light demand:								
L = 0, 1, 2	38.6 ± 14.7	76.4 ± 47.5*	35.6 ± 28.5	< *0.01*	18.7 ± 44.4*	134.5 ± 115.1	12.4 ± 23.7*	< *0.01*
L = 3, 4, 5	101.4 ± 30.9*	34.8 ± 17.6*	31.0 ± 15.0*	<*0.001*	32.8 ± 24.6*	46.7 ± 34.7	7.1 ± 4.6*	< *0.01*
L = 6, 7, 8	31.2 ± 25.3*	10.8 ± 18.0*	1.4 ± 1.8*	< *0.01*	78.5 ± 36.1*	120.5 ± 97.4*	17.7 ± 7.1*	< *0.001*
Mean number of identified seedlins	174.3 ± 41.9*	122.6 ± 53.8*	68.0 ± 34.0*	< *0.01*	154.7 ± 69.9	327.4 ± 169.9*	45.9 ± 45.3	< *0.001*

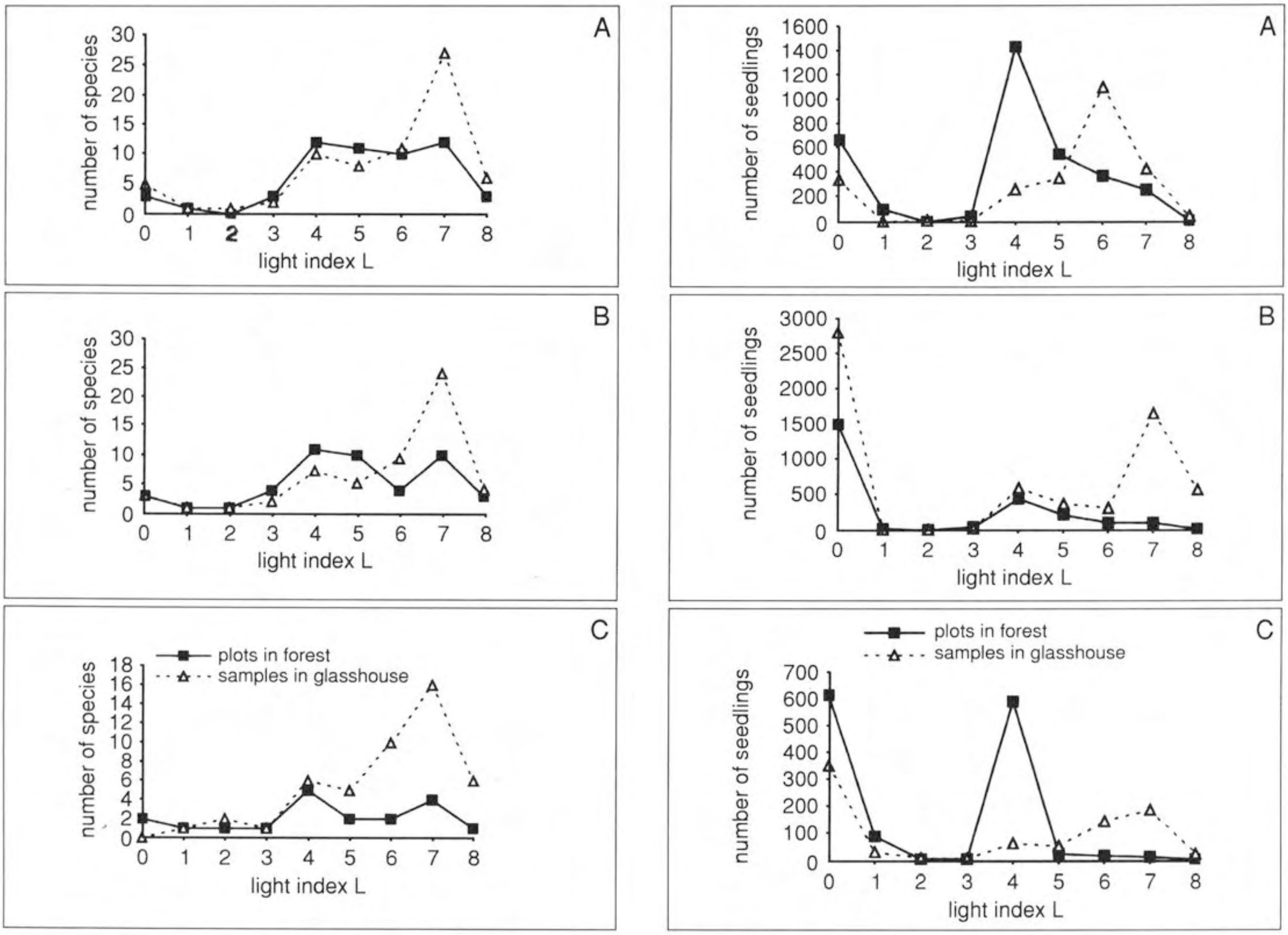

Fig. 3. Light requirements of the seed bank species whose seedlings emerged in the plots in the forest and soil samples in the glasshouse in the objects A, B, C during 3 seasons 1997-1999.

Light requirements of seedlings that emerged from the seed bank in the plots in the forest and soil samples in the glasshouse in objects A, B, C during 3 seasons 1997-1999 (description of the objects – Fig. 1).

as long-term observations require extra shelters of plots from possible seed rain and destruction. Having this in view, it becomes essential to prolong the observation period (in our study to 3 growing seasons) and to protect plots against a possible seed input (in our opinion the shelters we used served their turn, judging from a declining number of seedlings in the course of 3 seasons). Disquieting may seem the fact that seed bank estimated by seedling emergence in natural conditions is poorer in species and of smaller size in comparison with that in samples kept in a glasshouse. The difference in conditions in both cases is probably the bigger the more shady or less moist is the natural environment of a studied object.

We suppose that characteristics of the climate, when particular species composition of a given community formed, is important for the currently realised survival strategy of a species (for instance the Boreal Period with its cool but dry climate or the Atlantic Period with warm and moist climate).

Potentillo albae-Quercetum as a type of a community is regarded as a relict of the Atlantic Period (Faliński 1986). This community is distinguished from other natural forests by very high contribution (about 60%) of light- and warm-demanding species which are extremely rare in this latitude. In the Białowieża Primeval Forest these communities occupied the warmest habitats, seasonally dry owing to a very good dranaige. Insufficient soil moisture may limit seedling recruitment and growth in gaps in the herb layer formed by feeding deer, bisons or wild boars. The lower moisture and temperatures that currently characterise small gaps in the forest, especially in spring, comparing to the Atlantic Period, reduce the probability of seed germination and seedling emergence of high light-demanding species. The results of this study show that species richness of the seed bank realised in natural conditions is lower than that of the potential one. In the course of 3 seasons, in the forest, in the area of 2 m^2 there appeared seedlings of: A – 55, B – 48 and C – 19 taxa, whereas in the glasshouse – 76, 59 and 56, respectively. Although the size of the seed bank in the objects A and C turned out to be bigger in the plots (4385 and 1359 seedlings / 2 m^2) than in the soil samples (3093 and 918, respectively), this difference resulted from seedling emergence of only two species: *Anemone nemorosa* and *Carpinus betulus*. Only in the object B far fewer seedlings emerged in the plots than in glasshouse conditions (2459 and 6547 / 2 m^2). In this case as well the result was affected by enhanced recruitment of only one species, *Urtica dioica*, as much as 3 times lower in comparison with the soil samples.

In the warm moist environment of the glasshouse, from the seed bank there emerged species absent from the herb layer for more than 20 years (Kwiatkowska 1994a), such as: *Aquilegia*

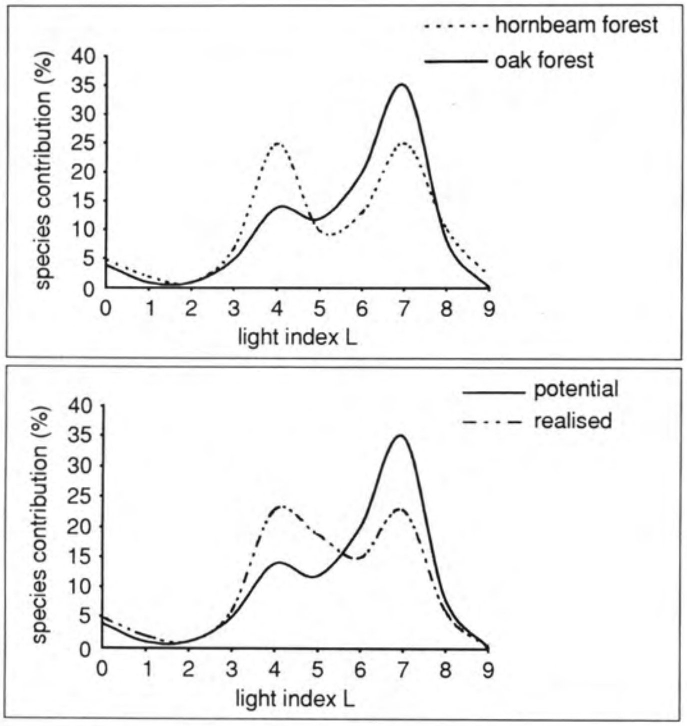

Fig. 4. The pattern of light requirements of species present in: a) the potential seed bank in the oak forest (*Potentillo albae-Quercetum*) and hornbeam forest (*Tilio-Carpinetum*), b) the potential and realised seed bank in the oak forest.

vulgaris, *Digitalis grandiflora*, *Gladiolus imbricatus*, *Hypericum montanum*, *Iris sibirica*, *Origanum vulgare*, *Ranunculus polyanthemos*, *Scorzonera humilis*, *Trifolium alpestre*.

Unfortunately, the conditions prevailing during 3 seasons in the forest (even in the least shaded part of the patch – A) were probably unsuitable for those species to appear in the experimental gaps in the herb layer. Contrarily, these conditions favoured seedling recruitment of moderately light-demanding forest species, that emerged much worse in the glasshouse. Among those were seedlings of both trees and shrubs typical of *Tilio-Carpinetum* (hornbeam forest), such as: *Acer platanoides**, *Carpinus betulus**, *Rubus saxatilis** and of many perennials: *Asarum europaeum*, *Hepatica nobilis**, *Lathyrus vernus**, *Majanthemum bifolium*, *Melampyrum nemorosum*, *Melittis melissophyllum*, *Mycelis muralis**, *Stellaria holostea** and *Ranunculus lanuginosus** (species found in the seed bank in the hornbeam forest by Pirożnikow 1983 are marked with an asterisk). In the plots better than in the glasshouse there emerged seedlings of such shade-tolerant species as *Anemone nemorosa** and *Oxalis acetosella**. Of those only *Luzula pilosa* had increased seedling density in the glasshouse. A second untypical species is *Urtica dioica** whose seedling emergence in the gaps in the herb layer is possibly reduced by low moisture of the soil.

Dissimilar environmental conditions in the plots in the forest and soil samples kept in the glasshouse select species at the seedling stage and cause the differences in patterns of light demand of species forming the realised and potential seed bank. In our previous study (Jankowska-Błaszczuk et al. 1998) we concluded that the pattern of light requirements of species present in the potential seed bank in the oak forest is described by an unimodal curve. The distribution is negatively skewed with maximum moved towards high values of the Ellenberg index L, similarly to the pattern of light demand of herb layer species. The pattern of the seed bank realised during 3 growing seasons in the oak forest is more similar to that of the potential one in the hornbeam forest than to the analogous pattern for the oak forest (Fig. 4). Although seeds of many high light-demanding species have lasted in the soil during the 20-year period of low light levels on the forest floor (which is visible in the results for the object C in the glasshouse), the species do not have a chance of seedling emergence in small gaps in the herb cover. They do, however, in bigger clearings in tree stand, which was the case in the object B. After cutting down the hornbeam undergrowth there had remained an expanded gap with much light reaching the herb layer for about 10 years. In the plots in this object there appeared seedlings of such species as: *Genista tinctoria*, *Hypericum maculatum*, *H. perforatum*, *Lathyrus pratensis*, *Trifolium repens* and *Vicia cracca*.

The presence of hornbeam undergrowth versus the size and species richness of seed bank

The results of this study show explicitly that the shading of the herb layer by the undergrowth of *Carpinus betulus* negatively affected the size and species richness of the seed bank. In the patch of oak forest studied the invasion by hornbeam began about 40 years ago. In this seasonally dry habitat hornbeam needs about 10 years to enlarge its root system so that it supplies the fast growing 11-12-year old saplings with enough water. *C. betulus* individuals at this age grow about 2 m high during a season. The tree felling that took place in winter 1979/1980 in the object B eliminated the ca. 20-year old undergrowth of the species. By that time its saplings had shaded the herbaceous vegetation for about 10 years since their recruitment to the shrub layer. On the one hand, the period of light depletion led to decreased frequency of high light-demanding species in the herb layer and a reduced seed input to the soil. As a consequence, the seed bank became smaller and less diverse. The long-term negative influence of hornbeam on the size and species richness of the seed bank in this community is most pronounced in the object C. On the other hand, increased density and diversity of the seed bank after cutting down the hornbeam undergrowth in the object B suggest that probably many seed bank species produce seeds viable in the soil for more than 10 years (e.g. *Digitalis grandiflora*, *Genista tinctoria*, *Erigeron annuus*, *Lathyrus pratensis*, *Origanum vulgare*, *Primula veris*, *Sagina procumbens*, *Betonica officinalis*, *Ajuga reptans*, *Astragalus glycyphyllos*, *Gnaphalium sylvaticum*, *Potentilla erecta*, *Lapsana communis*, *Thalictrum aquilegiifolium*, *Vicia sylvatica*) and require clearings in tree stand. Among those are also species from *Hypericum*, *Juncus* and *Rubus* genera that are commonly regarded as disturbance-dependent and forming long-term persistent seed banks.

The seed bank and probability to restore oak forest species with high light demand

The oak forests *Potentillo albae-Quercetum* are the richest in species natural forest communities in Poland. As Matuszkiewicz and Kozłowska (1991) reported in different regions of the country there were 60 to 100 herbaceous species per 100 m² on average. Comparing to that, in the seed bank samples with a total area of 2 m² taken in the best preserved patch of the oak forest and kept in unlimited light and moisture conditions of a glasshouse there emerged seedlings of as many as 76 taxa during 3 following seasons.

In the Białowieża Primeval Forest, like in the whole country, the oak forests gradually decline along with many extremely rare species (Faliński 1986, Jakubowska-Gabara 1993, Kwiatkowska 1986, 1994a, Kwiatkowska and Wyszomirski 1988, 1990). The possibility of their restitution by methods of active protection depends among others on species richness and longevity of seeds in the soil seed bank. Our study leads to the conclusion that a chance for high light-demanding species to reappear in the herb layer from the seed bank much decreases due to limited seed longevity in the soil after the 10-year shading by the hornbeam undergrowth. The active protection of these communities should be based on selective cutting down hornbeam along with controlled grazing by animals whose diet is dominated by shrubs and trees (Kwiatkowska 1996, Kwiatkowska and Wyszomirski 1988) and secondly, on forming small gaps in the herb layer, which would favour growth of forest herbs with moderate light demand.

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ZREALIZOWANY A POTENCJALNY BANK NASION W ZBIOROWISKU *POTENTILLO ALBAE-QUERCETUM* W PUSZCZY BIAŁOWIESKIEJ

STRESZCZENIE

Badania wschodów siewek z glebowego banku nasion prowadzono w ciągu 3 sezonów 1997-1999: 1) na 60 poletkach 0,1 m^2 w 3 obiektach: A – najlepiej zachowanym fragmencie dąbrowy z grabem obecnym jedynie w runie (zwarcie drzewostanu ok. 50-60%), B – w części płatu po eksperymentalnym wyrębie graba zimą 1979/1980 i ponownym wkroczeniu tego gatunku do warstwy krzewów (zwarcie >90%), C – w części płatu, w której grab jest obecny od 30-40 lat (zwarcie ok. 90%), oraz 2) w nie ogrzewanej szklarni w 60 próbach glebowych o jednostkowej powierzchni 0,1 m^2, pobranych z tych samych obiektów.

Wykazano, że bank nasion zrealizowany w warunkach naturalnych jest uboższy gatunkowo i mniej zasobny w siewki gatunków o wysokich wymaganiach świetlnych tj. $L \geq 6$ (na poletkach: A – 24; B – 17; C – 7, w szklarni odpowiednio: 44; 38; 32 gatunki / 2 m^2, na poletkach odpowiednio: 321; 108; 14, w szklarni: 785; 1205; 177 siewek / m^2). Większość typowych dla dąbrowy gatunków i ich siewek o wysokich wymaganiach świetlnych ujawnia się w warunkach szklarni. Na poletkach w lesie wschodzą głównie siewki gatunków umiarkowanie światłożądnych o $L = 3$-5 (na poletkach: A – 26; B – 25, w szklarni: 20; 14 gatunków / 2 m^2, na poletkach: 1014; 310, w szklarni: 328; 71 siewek / m^2). Zacienianie przez podrost graba wpływa negatywnie na zasobność banku nasion (na poletkach: A – 1743; B – 1226; C – 680; w szklarni odpowiednio: 1547; 3274 i 459 siewek / m^2) oraz na bogactwo gatunkowe: (na poletkach: A – 55, B – 48, C – 19; w szklarni odpowiednio: 76; 59 i 56 taksonów / 2 m^2).

Nazewnictwo: syntaksony – Matuszkiewicz (1981), taksony – Mirek i in. (1995).

SŁOWA KLUCZOWE: glebowy bank nasion, siewki w lesie, siewki w szklarni, inwazja graba.