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THE ROLE OF SEED BANK IN THE DYNAMICS OF UNDERSTOREY IN AN OAK FOREST IN HUNGARY

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We studied the potential role of seed bank in the dynamics of the understorey in a turkey oak-sessile oak forest *(Querceteum petraeae-cerris)* in Hungary. We used long-term records of the herb layer (1973–2006) and the seed bank composition of 2006 to assess the role of seed bank in the regeneration of herb layer. The total cover of herb layer decreased from 22% (1973) to 6% (1988), and remained low (<10%) till 2006; coinciding with the increasing cover of secondary canopy dominated by *Acer campestre*. We found a low density seed bank (ca. 1300 seeds/m^2). Altogether 33 species were germinated from the soil samples. A few generalist weed species composed the majority of seed bank. It was possible to assign a seed bank type for 19 species; 14 species out of 19 was long-term persistent. We found that the characteristic perennial forest herbs and grasses had only sparse seed bank. The Jaccard similarity between vegetation and seed bank was low (<30%). Our results suggest that the continuous establishment of forest herbs are not based on local persistent seed bank; it should be based on vegetative spreading and/or seed rain.

Keywords: Forest decay – herb species – seed density – seed persistence – seedling emergence

INTRODUCTION

The herb layer of forests has quick adaptation features which make it a sensible indicator of forest dynamical changes [1]. It is crucial to assess the composition and density of seed banks to understand dynamical events and predict the responses of the herb layer to disturbance [38, 52, 56, 62]. The seeds in the soil enable the plants to survive the unfavourable conditions for the germination and establishment [6, 23]. Furthermore, the seed bank can determine the direction of secondary succession after a disturbance [44] and can ensure information on the past and also predicts future changes [42]. The research of forest dynamics [17] and forest seed banks [e.g. 4, 27, 41] is in the centre of interest. But only a few studies compared seed bank composition with long-term herb layer records [33].

In our study long-term vegetation records of the herb layer (1973–2006) were compared with seed bank of 2006 in a turkey oak-sessile oak forest in Hungary. We aimed at to test the following hypotheses: (i) The seed bank is composed of a few

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generalist weed species; the characteristic perennial forest species do not form persistent seed banks [5, 22]. (ii) Species richness and seed density of seed banks are low; only a few short-lived species form a persistent seed banks [46, 55]. (iii) Similarity between the forest seed bank and present vegetation is low [48, 51]; the seed bank contains seeds of species characteristic to former composition of vegetation [6]; therefore, the seed bank is more similar to former stages of vegetation than to later ones.

MATERIALS AND METHODS

Site description and history

The study site was in the Síkfőkút Project Nature Reserve located ca. 6 km NE of town Eger, in the hilly region of North Hungarian Mountain Range (ca. 47°90'N; 20°46'E, a.s.l. 320–340 m). The climate is moderately continental with a mean annual temperature of 9.9 °C. The mean annual precipitation is between 500–600 mm, the yearly peak of precipitation is in the May–July period. Serious drought events were frequent during the studied period. The 64 ha reserve is vegetated with an even-aged ca. 100 years old xeric oak forest *(Quercetum petraeae-cerris)* [25]. One-third of the oak trees perished during the 1980s, and canopy gaps were formed [26, 39, 40]. These gaps were filled up by shrubs and also a dense second canopy was formed by *Acer campestre* [30, 31].

Sampling setup

Cover of vascular herb species were recorded in 33 permanent plots of 4 m × 4 m within a quarter-hectare sized area in July of the following years: 1973, 1982, 1988, 1994, 2000, 2006. Seed bank was sampled after natural winter stratification in the same plots after snowmelt in late March, 2006. In each plot 6 soil cores were collected (4 cm diameter and 10 cm depth, in a total volume of 25,000 cm^3). We treated the samples of all plots separately, which were divided in two vertical segments (0–5 cm, 5–10 cm). Identical segments drilled from the same plot were pooled. A bulk reduction procedure was used to reduce sample volume [53]. Vegetative organs were retained by washing over a coarse sieve (3.0 mm mesh). Seed-free fine soil components were removed on a 0.2 mm fine mesh. Sample volume was reduced by 65–70%. Volume reduced samples were spread in a 2–4 mm thick layer on 66 trays, formerly filled with 8 cm of steam-sterilized potting soil. Trays were placed under natural light in a greenhouse shaded with Rachel nets from early May to August. Temperature varied typically between 30 °C/18 °C at day/night. Seedlings were regularly counted, identified then removed [10]. Unidentified seedlings were transplanted. In early July, when no new seedlings emerged, watering was stopped; dried sample layers were crumbled and turned. In early September watering was re-started and continued till late October. Germination altogether lasted for 37 weeks. Seed rain as contamination was monitored in sample-free control trays filled with sterilized soil.

Data management

Raunkiaer life-forms and Grime's C-S-R strategy groups adapted to the Hungarian conditions (Social Behaviour Types) were used for the characterization of herbs [3]. Based on the Social Behaviour Types the followings were regarded as ruderals: AC-alien competitors, DT-disturbance tolerants, NP-natural pioneers, RC-ruderal competitors, W-weeds. We used transient, short-term persistent, and long-term persistent seed bank type classification of Thompson et al. [56]. Species with less then three seeds in the samples (less than a density of 12 seeds/m^2) were not classified.

Spearman rank-correlation was used to compare the species ranks of the cover of herbaceous species [49]. Similarity of the seed bank and vegetation data was displayed by nonmetric multidimensional scaling [35]; similarity was calculated by the Jaccard similarity. Differences between years in means of cover and species numbers were tested using RM ANOVA and in case of significant differences Tukey test was used [62].

RESULTS

Understorey vegetation

Altogether 53 vascular species were recorded in vegetation; out of these 15 species were recorded only once during the whole study period. The species composition changed substantially during the study period (Table 1). Several characteristic forest herbs (e.g. *Carex michelii*, *C. montana*, *Lathyrus niger*) were typical in the vegetation recording before 1988. From 1988 onwards only sparse cover of forest species were detected *(Lathyrus vernus, Melica uniflora, Poa nemoralis).* Several nitrophytes were established permanently during the studied period (e.g. *Alliaria petiolata*, *Chelidonium majus*, *Galium aparine* and *Geranium robertianum*). The mean cover of the herb layer was 22% in 1973. This score was decreased below 10% and remained low till the end of the study (Table 2). The mean number of species significantly decreased from 1973 to 1988 ($p<0.001$), but we found significant increase from 1988 to 2006 ($p<0.001$, Table 2). We found that the species ranks also changed significantly ($p<0.001$). The cover of perennial graminoids (e.g. *Poa nemoralis* and *Melica uniflora*, *Carex* spp.) decreased remarkably. From 1994 onwards the cover of nitrophilous annuals and short-lived ruderals (e.g. *Chelidonium majus*, *Fallopia dumetorum*, *Geranium robertianum*) were increased (Table 1).

Table 1
Percentage cover (mean ± SE) of the most frequent 25 species during the studied period

Species	SBT	FS	1973	1982	1988	1994	2000	2006
Carex michelii	G	PG	5.9±1.1	3.4±0.8	0.3±0.2			
Carex montana	S	PG	2.8±0.9	1.4±0.5				
Dactylis polygama	G	PG	1.7±0.3	1.0±0.2				
Fragaria vesca	G	PH	0.4±0.1	0.2±0.1				
Festuca heterophylla	C	PG	1.1±0.4	0.4±0.1				
Galium schultesii	G	PH	1.5±0.7	1.2±0.5	1.2±0.7			
Lathyrus niger	G	PH	0.5±0.2	0.4±0.1				
Melica nutans	G	PH	0.4±0.2	0.2±0.1				
Melica uniflora	C	PG	1.4±0.7	0.8±0.3		0.5±0.3	0.3±0.2	
Poa nemoralis	C	PG	4.6±1.1	2.5±0.6	0.5±0.3	0.2±0.2	0.1±0.1	
Alliaria petiolata	DT	PH			0.2±0.1		0.1±0.1	
Carex muricata	DT	PG			0.2±0.1			0.3±0.1
Galium aparine	W	AH			0.2±0.1	0.5±0.3	0.2±0.1	1.9±0.8
Geranium robertianum	DT	AH			1.1±0.8	0.5±0.2	0.1±0.1	1.4±0.9
Lathyrus vernus	S	PH			0.2±0.1	0.1±0.1	0.3±0.1	0.2±0.1
Fallopia dumetorum	DT	AH			0.5±0.1	0.8±0.3	0.3±0.2	0.2±0.1
Symphytum nodosum	G	PH			0.2±0.1			
Chelidonium majus	W	PH				0.8±0.5	0.1±0.1	1.3±0.7
Melittis grandiflora	G	PH				0.1±0.1		
Polygonatum latifolium	G	PH				0.3±0.2	0.4±0.4	0.7±0.5
Veronica chamaedrys	DT	PH				0.1±0.1		
Dictamnus albus	S	PH					0.1±0.1	
Ajuga reptans	DT	PH						0.2±0.1
Stachys sylvatica	G	PH						0.2±0.1
Stellaria media	DT	AH						0.2±0.1

Notations: Social Behaviour Types (SBT, [3]): C – competitors, DT – disturbance tolerants, G – generalists, W – weeds, S – stress tolerants. Functional species groups (FS) based on morphological categories and Raunkiaer's Life-form system: PG – perennial grass, PH – perennial herb, AH – annual herb.

Table 2
Change of vegetation cover and species richness (mean ± SE) in the study period

	1973	1982	1988	1994	2000	2006
Cover	$22.3±3.2^{a}$	$12.2±1.9^{b}$	$5.6±1.3^{c}$	$4.0±0.8^{d}$	$1.8±0.5^{e}$	$7.9±1.4^{f}$
Species richness	$5.8±0.4^{a}$	$5.5±0.4^{a}$	$2.4±0.3^{b}$	$1.8±0.3^{c}$	$1.0±0.3^{d}$	$4.2±0.6^{e}$

Different superscripted letters refer significant differences between years (RM-ANOVA, $p < 0.001$).

Table 3
Seed bank composition of the 33 plots in the upper (0–5 cm) and lower (5–10 cm) soil layer (seeds/m^2)

Species	SBT	FS	0–5 cm	5–10 cm	P
Ajuga reptans	DT	PH	24	36	3
Ballota nigra	W	PH		4	
Fallopia dumetorum	DT	AH	8	4	2
Carex michelii	G	PG	12		1
Carex muricata	DT	PG	56	68	3
Chenopodium album	RC	AH	52	8	3
Chenopodium hybridum	W	AH	4		
Chenopodium polyspermum	RC	AH	133	193	3
Cherophyllum temulum	DT	AH		4	
Cirsium arvense	RC	PH	4		
Cirsium vulgare	W	PH	32	4	3
Conyza canadensis	AC	AH	48	28	2
Dactylis glomerata	DT	PG	8	4	3
Epilobium montanum	G	PH	8		
Epilobium tetragonum	G	PH	4		
Festuca heterophylla	C	PG	4		
Fragaria vesca	G	PH	24	4	3
Hypericum perforatum	DT	PH	52	52	3
Lathyrus niger	G	PH	4		
Matricaria maritima	W	AH	4		
Melandrium album	W	AH	4		
Melica uniflora	C	PG	4		
Poa nemoralis	C	PG	44	20	2
Polygonum lapathyfolium	DT	PH	4	4	
Solanum nigrum	W	AH	4	8	3
Stellaria media	DT	AH	40	36	3
Taraxacum officinale	RC	PH	4		
Turritis glabra	G	PH	8	4	3
Typha angustifolia	C	PH	52	24	3
Urtica dioica	DT	PH	8		
Verbascum nigrum	G	PH	4	36	3
Veronica chamaedrys	DT	PH	36	8	2
Vicia lathyroides	NP	AH	8	8	3

Abbreviations and notations: the Social Behaviour Types (SBT) categories by Borhidi [3]: AC – alien competitors, DT – disturbance tolerants, G – generalists, NP – natural pioneers, RC – ruderal competitors, W – weeds. Functional species groups (FS): PG – perennial grass, PH – perennial herb, AH – annual herb. The seed bank types (P) of species according to the system of Thompson [56]: 1 – transient; 2 – short-term persistent; 3 – long-term persistent.

Seed bank

Altogether 33 species (7 monocots and 26 dicots) emerged from the soil samples. We detected a mean seed density of 1.270 seeds/m^2. Significantly higher number of seeds were detected in the upper soil layer than in lower one ($p < 0.05$). Altogether 44% of the total seed bank was detected in the lower layer (Table 3). A limited number of species comprised the majority of seed bank. Ten species formed the 80% of total seed bank. *Chenopodium polyspermum* had the highest seed density (ca. 330 seeds/m^2). The proportion of ruderals in total seed density was high (about 80%). Out of the perennial graminoids only *Poa nemoralis* (ca. 64 seeds/m^2) and *Carex muricata* (ca. 125 seeds/m^2) built up detectably dense seed bank. Most of the detected species had at most sparse seed banks (Table 3). Lower than the half of the detected species in the present vegetation (2006) had some seed bank. Altogether for 19 species was possible to assign a seed bank type, and most of them had long-term persistent seeds (14 species).

Herb layer and seed bank

During the whole study period (vegetation 1973–2006 and seed bank in 2006) 158 species were detected. There were 17 species in the seed bank which were not recorded in the vegetation. Among these species *Chenopodium album* and *Typha angustifolia* were the most frequent, but with low mean density (60 and 76 seeds/m^2, respectively). We found that 37 species of herb layer did not form detectably dense seed

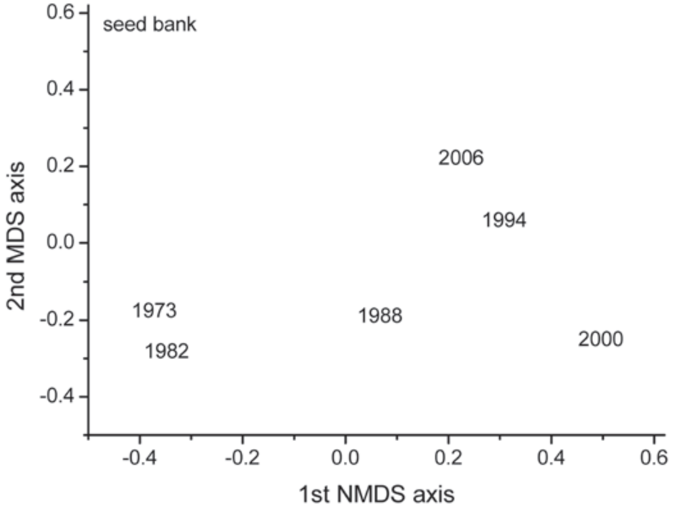

Fig. 1. Nonmetric multidimensional scaling of the species composition of the seed bank and the herbaceous vegetation based on Jaccard similarity (stress = 0.27)

bank. Several among them were characteristic forest species detected frequently in the vegetation (*Melica nutans*, *Polygonatum latifolium*, *Stachys sylvatica*, and *Viola hirta*). Several species (e.g. *Chelidonium majus* and *Geranium robertianum*) detected in vegetation did not form any seed bank (Table 3).

In 2006, 53 species composed the vegetation and the seed bank. Among them 20 species were found exclusively in the vegetation, while 18 species only in the seed bank. There were 15 species both in the vegetation and in the seed bank. The Jaccard similarity between vegetation of the studied years and the seed bank was low (ranged from 11% to 28%; Fig. 1). Higher scores than 20% were only detected between seed banks and the vegetation records of 1973 and 2006, respectively.

DISCUSSION

Density and richness of seed bank

Compared to the literature the detected mean seed density of 1.270 seeds/m^2 is low. In the broadest sense, in dry-mesophilous grasslands several thousand seeds per square meter is typical [59]; in wet meadows and dry psammophilous grasslands even higher figures are common [37, 38, 57]. In former studies in forest seed banks a wide range of density scores were found. Typical seed density in most of the studies range from several hundred to several thousand seeds per m^2 in the top 10 cm [11, 24]. Schiffman and Johnson [48] found less than one seed/m^2 in different stands of Virginian oak forests. In mature beech forests there were found from 1,400 to 21,500 seeds/m^2 [50] and 12,400 seeds/m^2 in an oak-beech forest of Belgium [5]. In an old-growth temperate deciduous forest of Quebec there were from 475 to 16,700 seeds/m^2 [34]. Kjellsson [29] found from 2,200 to 15,600 seeds/m^2 in Danish deciduous forests. The species richness in the seed bank found in our study, compared to former ones was high (33 species). Godefroid et al. [19] found 9–24 species in temperate forest ecosystem, and only 9–11 species were typical in *Quercus* spp. dominated stands. In mixed coniferous forest Zobel et al. [62] detected 13–29 species.

Species composition of seed banks

We found that 80% of forest seed bank was composed by ruderals. This is well in accordance with the results of previous studies [4, 29, 46]. It was formerly found that, the seed bank of temperate forests was mainly composed by early successional species (characteristic species to clearings), ruderals [4, 5, 22] or rarely by invasive species [22]. For typical species of undisturbed habitats, only short term persistence was proven [42, 58].

The most frequent species was a long-term persistent seeded weed, *Chenopodium polyspermum*. This species is a shade intolerant weed, characteristic to open agricultural areas, and were not detected in the vegetation. As formerly published, the seed bank density of *Chenopodium* species can exceed 10,000 seeds/m^2 [16]. Seeds of *Chenopodium polyspermum* – can successfully persist several decades [7, 9, 20, 21, 23, 47]. On the other hand, it is more likely that the detected weed seeds are originated from the surroundings by spatial dispersal. Closely to the studied forest stand abandoned vineyards are situated, where this species is frequently recorded.

Many authors suggest that the most shade-tolerant species do not form a persistent seed bank [e.g. 4, 22]. Our results support these findings; we found that the seed bank of perennial forest grasses and forbs were sparse. The low seed density of these species can be explained with predation, because seeds of late successional species are large and they are more frequently exposed to predation, than small seeded, early successional ones [12, 18]. Moreover, perennial grasses and forbs often could survive strong shading [28]. In such conditions the regeneration and spreading most of the perennial forest species is more likely based on vegetative spreading and reproduction than on seed bank formation [36].

Our third hypothesis was that there is a poor similarity between the present forest vegetation and seed bank composition [54, 60]. As it was presented in the review of Bossuyt and Honnay [6], that the species similarity between seed bank and vegetation across ecosystems was the lowest in forests with a mean score around 30%. In our study only lower scores were found than that. The main causes of low similarity between vegetation and seed banks of the forests are: (i) Persistent seeds of ruderal species remain viable in the soil for a long time without germination [5, 8, 13, 32]. (ii) In low density seed banks, species with small amounts of short-lived seeds with clumped horizontal pattern can remain undetected by sampling. (iii) Presence of several hygrophytes (e.g. *Typha angustifolia*) exclusively in seed bank is a further source for dissimilarity.

The soil seed bank of the studied oak forest contains many persistent seeds of ruderal species. Conversely, characteristic forest grasses and forbs do not possess dense seed banks. As a consequence, the recovery of former understory typical in the early years of the study (1973–1988) is difficult from local seed banks. There are some other driving forces such as the increased vegetative propagation [14, 15] and seed rain from adjacent areas which have more important influence on the regeneration dynamics of understory in temperate forests than persistent seed bank formation. Our results suggest that the continuous establishment of forest herbs are not based on local persistent seed bank; it should be based on vegetative spreading and/or seed rain.

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