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ORIGINAL RESEARCH PAPER

Necromass as seed reservoir in macroforb meadows with varied moisture conditions

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Abstract

Necromass, i.e., dead plant parts, has a great impact on the spatial patterns of populations and communities. Depending on its thickness and the degree of decomposition, it may constitute a space-blocking physical barrier and impede recruitment of individuals due to, e.g., autotoxication. The aim of the study was to determine the role of the necromass layer in formation of the soil seed bank of variously moist meadow communities and its influence on the efficiency of generative reproduction. The authors paid special attention to the possibility of capture and storage of seeds of species occurring in the vegetation cover by necromass. Additionally, selected features of seeds of species present on the necromass were analyzed in order to identify species that can potentially contribute to formation of the necromass seed bank.

The plant cover comprised 52 species in total. Seedlings of 21 taxa appeared on the necromass and their number ranged from 10 to 13, depending on the patch. The density of the seedlings ranged from 339 to 4923 m⁻². In all patches, *Lythrum salicaria* and *Lysimachia vulgaris* seedlings were most numerous. These two species were characterized by the highest frequency as well. The low values of Jaccard's index (0.28–0.36) imply a low share of taxa that are common for the necromass and the vegetation cover. This result should be explained by the occurrence of large disproportions in the number of all species identified on the necromass and among the vegetation. The seeds are typically characterized by small sizes and usually have smooth or finely striated and/or ribbed surface texture. The presence of additional structures, e.g., pappus and hairs, in the largest and heaviest seeds (*Crepis paludosa*, *Geum rivale*, and *Cirsium* spp.) may help seeds capture in the necromass.

Keywords

macroforb meadow; necromass; seed bank; seedlings emergence; vegetation

Introduction

Dead plant parts have a great impact on the spatial patterns of populations and communities. Necromass represents a layer on the border between biotic and abiotic factors. Dead plant parts usually form a compact, persistent cover. Its decomposition rate is determined by both the type of the constituent plant material and the prevailing habitat conditions, primarily the moisture levels, which have the greatest contribution to oxygen availability [1,2]. Depending on its thickness and the degree of decomposition, necromass may be a space-blocking physical barrier and impede recruitment of individuals due to, e.g., autotoxication [3–6]. Plant litter may affect the timing of

germination and establishment of many plant populations. Experimental manipulations of litter demonstrated its impact on plant community structure and interspecific interactions [2,7–12]. The origin of the necromass may affect seed germination in different way depending on its physical structure [13,14]. Necromass of grass origin, which is interwoven thread-like structure, may have a more negative effect on emergence than the presence of necromass composed of small flat pieces, e.g., formed of deciduous tree leaves. Processes of seeds germination and establishment of new individuals which respond to these different necromass characters may also vary with the species origin. Grassland species seem to be more adapted to and more tolerant of grass necromass than for example woodland necromass [13,14].

Grime [15] considers persistent litter to be one of the features of the competitive strategy. Appearance of plant seedlings is not only influenced by dead parts of vascular plants. For example, during the establishment phase, the moss layer plays an important role [16,17]. Seed germination conditions are remarkably worse here than on the soil surface. Seedlings emerge only in favorable light, thermal, and moisture conditions [18–20]. The necromass layer modifies microhabitat conditions. Substantial amounts of accumulated dead plant parts reduce the intensity of evaporation from the soil surface. Such microhabitats are characterized by higher moisture and, concurrently, a higher degree of shading. Low necromass amounts may have the same effect as a vegetation canopy with respect to temperature amplitude, thus improving microclimate conditions. With water deficit in the soil, necromass can promote more intensive seed germination and seedling survival rates [10]. It seems that low amounts of litter may improve microsite conditions, thereby increasing seedling growth even when competitors are present [21]. Additionally, there may be an indirect positive effect of necromass on seedling emergence and growth, if the necromass cover reduces the growth and biomass of competitors. In contrast, high necromass amounts may exert negative effects that add to the negative effects of competition, particularly under moist conditions [22,23].

Similar to soil, necromass has its own seed bank. Some seeds remain in the necromass only temporarily and can enter the soil seed bank over time [24]. Morphological traits of diaspores (seeds or fruits) are one of the most important factors determining the potential of a species to contribute to the necromass seed bank. The seed size is one of the adaptations of species to the growing conditions. It is a measure of plant's investment in generative reproduction. In turn, the seed shape is clearly related to the type of the seed bank. Small, light, and smooth seeds devoid of additional structures usually form a persistent seed bank, as they can penetrate the soil more easily and their germination is typically initiated by different spatial- and temporal-scale disturbances [24,25]. Species with smaller seeds are generally inhibited by necromass to a substantially larger extent than species with larger seeds, either in the germination or seedling stages. Seeds with an elongated shape and irregular texture, additionally equipped with, e.g., hooks, hairs, or pappus, have an impeded access to the soil surface through the necromass filter [24,26].

The aim of the study was to determine the role of the necromass layer in formation of the soil seed bank and its influence on the efficiency of generative reproduction. The authors paid special attention to the possibility of capturing and storage by necromass of seeds of species occurring in the vegetation cover. Additionally, selected features of the seeds of species present in the necromass were analyzed (biometry, shape, depth distribution and longevity indices, and persistence) in order to identify species that can potentially contribute to formation of the necromass seed bank.

The following research hypotheses were put forward: *(i)* necromass restrains the seed flow into the soil; *(ii)* necromass is a suitable substrate for seed germination; *(iii)* necromass is a germination substrate primarily for seeds with additional structures (e.g., pappus, hairs), which facilitate persistence of the seeds on the necromass.

Material and methods

The research was carried out in the Szum River valley in the Central Roztocze region, SE Poland. The study area comprises hydrogenic habitats in a waterlogged terrace

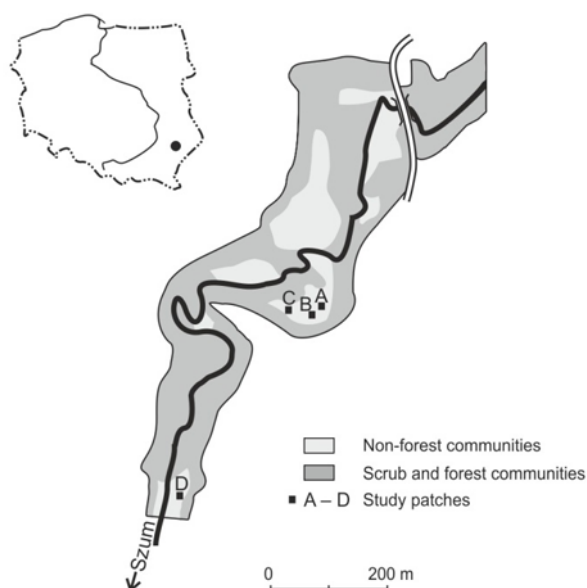


Fig. 1 Study area in the Szum River valley (Czarnecka [28], slightly changed).

inhabited by a mosaic of meadow communities of the *Molinio-Arrhenatheretea* class and *Magnocaricion* rushes of the *Phragmitetea* class [27–29]. Four patches of variously moist macroforb meadows of the *Molinio-Arrhenatheretea* class were chosen for the investigations: *Lysimachio vulgaris-Filipenduletum* – Patches A and D, *Cirsietum rivularis* – Patch B, and *Lythro-Filipenduletum ulmariae* – Patch C (Fig. 1). In the 2005 growing season, floristic inventories were made in each patch. An 11-grade species cover scale (“+” for a species with cover less than 5%, “1” for cover 5–10%, “2” – 11–20%, ..., “10” – 91–100%) was used. In the early spring of 2006, 12 necromass samples were taken from the total area equal to 1 m² in each patch. The material was placed in cuvettes, which were transferred to a cold frame in the experimental garden and watered regularly. During 20 months, systematic emergence of seedlings was observed, which were removed after identification using available literature [30,31]. In the case of identification problems, the seedlings were transplanted into a separate container and observed further until emergence of morphological characteristics that allowed identification of the taxon.

The Shannon–Wiener and evenness indices were used to evaluate the biodiversity of the vegetation and necromass seed bank. The qualitative similarity between the vegetation and necromass samples was calculated using Jaccard’s index and the quantitative similarity was assessed with Spearman’s rank correlation coefficient [32,33]. In these calculations, the number of seedlings that emerged on the necromass was converted into their percent share with an 11-grade scale, as in the case of vegetation. The frequency of all the taxa noted on the necromass sampled from each patch was calculated using a four-grade scale: I – taxa present in less than 25% of all samples, II – 26–50%, III – 51–75%, and IV – 76–100%.

The following biometric features were determined for the seeds of each species germinating on the necromass: length, width, weight [34,35], surface texture, and presence of appendages [36]. Based on these parameters: the variance of seed dimensions (shape index), depth distribution and longevity indices [37], and persistence of diaspores [25] were determined. Seed shape (V_s) was measured as a variance of the length, width, and thickness of seeds, after all the values had been transformed for the length to equal one [37]. In this way, the shape becomes dimensionless and can vary between 0 (perfectly spherical) and 0.2 (shaped like a thin disk or a slim needle). Depth distribution (D) was measured according to Bekker et al. [37]:

$$D = -504.9 \log(M) - 498.9 \log(\sqrt{V_s}) + 521.1 \log(M\sqrt{V_s}) + 94$$

where: M – seed mass, V_s – variance of seed dimensions (seed shape).

The relationship between the horizontal distribution of seeds in the soil and their persistence was measured according to the formula of Bekker et al. [37]:

$$L = -0.003023 D - 0.2065 \log(M\sqrt{V_s}) + 0.3938$$

The longevity index (L) ranged from 0 (seeds classified as transient) to 1 (those categorized as persistent). The analyzed species were classified according to the theoretical method of seed longevity estimation [25]. The diaspores whose weight did not exceed 3 mg and whose seed shape was smaller than 0.18 were classified as persistent, while those heavier than 3 mg and with greater variance – as transient.

The nomenclature of the vascular flora follows Mirek et al. [38] and the classification of plant communities follows Matuszkiewicz [39]. Statistical calculations were performed with the help of the Statistica 8 software package [33].

Results

Species richness and the biodiversity of the vegetation and necromass seed bank

In total, from 27 (Patch D) to 40 (Patch B) vascular plant species were found in the analyzed vegetation patches. The plant cover comprised 52 species. The meadow vegetation was dominated by macroforbs: *Filipendula ulmaria*, *Lythrum salicaria*, *Lysimachia vulgaris*, *Cirsium oleraceum*, and sedge – *Carex acutiformis* (Tab. 1, Tab. 2). Seedlings of 21 taxa appeared in the necromass and their number ranged from 10 to 13, depending on the patch (Tab. 2, Tab. 3). The necromass layer in the study communities was primarily formed by dead shoots of *C. acutiformis* and macroforbs *C. oleraceum*, *F. ulmaria*, and *L. vulgaris*. The Shannon–Wiener’s index calculated for the taxa noted in the vegetation exhibited values in the range of 1.28–1.46 and a clear correlation with the species richness (Tab. 2). The very small differences in the evenness index indicated similar quantitative relationships between the species noted in the analyzed patches. In the case of the necromass, the above indices exhibited comparable values in three of the analyzed patches – A, B, and D. Despite the greatest density of seedlings, the seed bank in Patch C was characterized by clearly lower biological

Tab. 1 General characteristics of the vegetation of study patches.

	Patches			
	A	B	C	D
Association	<i>Lysimachio vulgaris-Filipenduletum</i> Bal.-Tul. 1978	<i>Cirsietum rivularis</i> Nowiński 1927	<i>Lythro-Filipenduletum ulmariae</i> Hadač et all. 1997	<i>Lysimachio vulgaris-Filipenduletum</i> Bal.-Tul. 1978
Dominant species / cover scale*	<i>Filipendula ulmaria</i> (L.) Maxim. /5 <i>Carex acutiformis</i> Ehrh. /4 <i>Lysimachia vulgaris</i> L. /4 <i>Lythrum salicaria</i> L. /3 <i>Cirsium oleraceum</i> (L.) Scop. /2 <i>Geum rivale</i> L. /2 <i>Mentha longifolia</i> (L.) /2	<i>Cirsium rivulare</i> (Jacq.) All. /5 <i>Filipendula ulmaria</i> (L.) Maxim. /5 <i>Carex acutiformis</i> Ehrh. /4 <i>Lysimachia vulgaris</i> L. /3 <i>Lythrum salicaria</i> L. /3 <i>Cirsium oleraceum</i> (L.) Scop. /2 <i>Cirsium palustre</i> (L.) Scop. /2 <i>Geum rivale</i> L. /2 <i>Lychnis flos-cuculi</i> L. /2 <i>Mentha longifolia</i> (L.) L. /2	<i>Filipendula ulmaria</i> (L.) Maxim. /5 <i>Carex acutiformis</i> Ehrh. /4 <i>Lythrum salicaria</i> L. /4 <i>Cirsium oleraceum</i> (L.) Scop. /3 <i>Lysimachia vulgaris</i> L. /3 <i>Geum rivale</i> L. /2 <i>Peucedanum palustre</i> (L.) Moench /2 <i>Thelypteris palustris</i> Schott /2	<i>Filipendula ulmaria</i> (L.) Maxim. /5 <i>Carex acutiformis</i> Ehrh. /4 <i>Lysimachia vulgaris</i> L. /4 <i>Cirsium oleraceum</i> (L.) Scop. /2 <i>Geum rivale</i> L. /2 <i>Lythrum salicaria</i> L. /2

* The cover scale was explained in the chapter “Material and methods”.

Tab. 2 Differentiation of number of taxa, Shannon–Wiener and evenness indices in the vegetation and necromass seed bank.

	Patches							
	vegetation				necromass			
	A	B	C	D	A	B	C	D
Number of taxa	30	40	33	27	12	13	12	10
Shannon–Wiener index	1.34	1.46	1.37	1.28	0.95	1.00	0.65	0.91
Evenness index	0.89	0.90	0.88	0.87	0.88	0.89	0.60	0.88

Tab. 3 Abundance, percentage distribution, and frequency of seedlings of taxa recorded on the necromass (No. of seedlings m⁻²).

Taxon	Patch A			Patch B			Patch C			Patch D		
	Σ	%	Fr.	Σ	%	Fr.	Σ	%	Fr.	Σ	%	Fr.
<i>Carex acutiformis</i> Ehrh.	16	3.7	II	12	3.3	II	15	0.3	II	37	10.9	III
<i>Cirsium oleraceum</i> (L.) Scop.	42	10.0	II							9	2.7	I
<i>Cirsium palustre</i> (L.) Scop.	4	0.9	I	9	2.5	I	25	0.5	I			
<i>Cirsium rivulare</i> (Jacq.) All.				22	6.1	II						
<i>Crepis paludosa</i> (L.) Moench							5	0.1				
<i>Filipendula ulmaria</i> (L.) Maxim.	17	4.0	III	22	6.1	III	20	0.4	II	19	5.6	II
<i>Galium uliginosum</i> L.				8	2.2	I				14	4.1	II
<i>Geum rivale</i> L.	6	1.5	I				15	0.3	II			
<i>Juncus effusus</i> L.	135	32.1	IV							47	13.9	III
<i>Lotus uliginosus</i> Schkuhr				12	3.3	I						
<i>Luzula luzuloides</i> L.	4	0.9	I									
<i>Lychnis flos-cuculi</i> L.				32	8.8	I						
<i>Lycopus europaeus</i> L.	14	3.3	I							12	3.5	I
<i>Lysimachia vulgaris</i> L.	60	14.2	IV	47	12.9	IV	69	1.4	IV	61	18.0	IV
<i>Lythrum salicaria</i> L.	70	16.6	IV	121	33.3	IV	4648	94.4	IV	86	25.4	IV
<i>Mentha longifolia</i> (L.) L	38	9.0	III	22	6.1	II				17	5.0	II
<i>Myosotis palustris</i> (L.) L. Emend. Rchb.							8	0.2	I			
<i>Peucedanum palustre</i> (L.) Moench							9	0.2	I			
Poaceae				28	7.7	I	34	0.7	II	25	7.4	III
<i>Potentilla erecta</i> (L.) Raeusch.				12	3.3	I	30	0.6	II			
<i>Scutellaria galericulata</i> L.	16	3.8	I	8	2.2	I	21	0.4	II			
Non-identified				8	2.2	I	24	0.5	I	12	3.5	I
Total number of seedlings	422			363			4923			339		

Fr. – frequency: I – ≤ 25%, II – 26–50%, III – 51–75%, IV – 76–100% of samples.

diversity and uniformity. This was caused by the very high proportion of seedlings of one species – *L. salicaria*. In all patches, *L. salicaria* and *L. vulgaris* seedlings were most numerous (Tab. 3). Taxa represented by an equally large number of seedlings in the analyzed patches included *C. oleraceum*, *Juncus effusus*, *Lychnis flos-cuculi*, and representatives of Poaceae. The density of seedlings in Patches A, B, and D (*Lysimachia vulgaris*-*Filipenduletum* and *Cirsietum rivularis* communities) ranged from 339 to 422 m⁻². Substantially higher numbers of seedlings (4923 m⁻²) were identified in the *Lythro-Filipenduletum ulmariae* patch, with 94% of *L. salicaria* seedlings. The most abundant species (*L. salicaria* and *L. vulgaris*) exhibited the highest frequency. Seedlings of *C. acutiformis* and *F. ulmaria* appeared in all patches, although with a lower frequency (Tab. 3).

The low values of Jaccard's index (0.28–0.36) imply a low share of taxa that are common for the necromass and the vegetation cover (Tab. 4). Only one of the taxa

Tab. 4 Comparison of the structure of the vegetation and necromass seed bank using Jaccard's index and Spearman's rank correlation coefficient.

	Patches			
	A	B	C	D
Jaccard's index	0.35	0.32	0.28	0.36
Spearman's coefficient	0.60; $p < 0.001$	0.42; $p < 0.01$	0.22; n.s.	0.39; $p < 0.05$

noted in the necromass did not occur simultaneously in the plant cover. This was the *Luzula luzuloides* species, whose diaspores germinated on the material originating from Patch A. A positive correlation was shown between the shares of the individual species in the plant cover and necromass. The highest value of Spearman's rank correlation coefficient was noted for Patch A ($r = 0.60$) and the lowest value ($r = 0.22$) was calculated for Patch C.

Features of seeds identified on the necromass

The seeds of the identified species were characterized mainly by small sizes. *Galium uliginosum*, *J. effusus*, *L. flos-cuculi*, *L. salicaria*, and *Mentha longifolia* had smallest seeds; therefore, they had a potentially strong chance to be captured on the necromass filter (Tab. 5). *Carex oleraceum*, *C. palustre*, *C. rivulare*, *F. ulmaria*, *Geum rivale*, and *Peucedanum palustre* produced the largest seeds. The size of the seeds was positively correlated with their weight. The seeds of the largest species reached a weight over 2 mg.

The shape index calculated from the seed size and weight was in the range from 0.004 to 0.275 (Tab. 5). *Lotus uliginosus*, *L. flos-cuculi*, *Potentilla erecta*, and *Scutellaria galericulata* produced seeds with a most spherical shape. Species with shape index values over 0.2 produced more elongated diaspores (i.e., *Crepis paludosa* and *G. rivale*). The seeds of a majority of the analyzed species had smooth or finely striated and/or ribbed surface texture. Additional structures such as pappus and hairs, which promote capture of seeds on the necromass layer, were only noted in *C. paludosa*, *G. rivale*, and species from the genus *Cirsium*.

The depth distribution index was in the range of 51.17–93.08. The higher the value of this index, the greater the likelihood of seed presence in the surface layer of soil was. It was found based on these results that *J. effusus* diaspores had the greatest ability of all seeds that reached the soil surface to penetrate deeper into the soil profile. This species also achieved the highest value of the longevity index ($L = 0.754$), which suggests that it is able to form a persistent seed bank. A majority of the species were able to form a persistent seed bank (Tab. 5, Fig. 2), which is indicated by the low values of diaspore weight (<3 mg) and shape index ($V_s < 0.18$). Taxa whose morphological characteristics of seeds contribute to formation of a seed bank with lower persistence comprise *C. oleraceum*, *C. paludosa*, *F. ulmaria*, *G. rivale*, and *P. palustre*. The major determinant of seed persistence in these species is the irregular, elongated shape of the seeds.

Discussion

The probability of sustenance and development of a population increases if new genets appear at least from time to time. Environmental conditions prevailing in the population habitat may influence the process of recruitment of new individuals by modification of traits determining individual fertility, e.g., the ability to produce generative shoots, the number of inflorescences, or the sum of produced viable seeds, and by creation of favorable conditions for diaspore germination and seedling growth [40].

The analyzed meadow communities are characterized by a large share of macroforb species and sedges, which exhibit substantial gains in the biomass of aboveground parts. The authors have noted the greatest thickness of necromass at the end of the growing season, i.e., at the turn of October and November. In late fall, the ground surface is dominated by newly dead aboveground plant parts. In early spring, the layer is usually less thick, as it is pressed by the snow cover during the winter time (Franczak, unpublished). It can be assumed that the density of seedlings

Tab. 5 The features of seeds identified on necromass.

Species	Length (mm)	Width (mm)	Height (mm)	Weight (mg)	Shape index (V_s)	Surface texture	Appendages	Depth distribution index (D)	Longevity index (L)	Persistence*
<i>Carex acutiformis</i>	3.50	1.65	1.10	1.11	0.129	Smooth		84.86	0.224	Persistent
<i>Cirsium oleraceum</i>	4.42	1.65	0.75	2.50	0.187	Glabrous or slight striate	Pappus	92.36	0.112	Transient
<i>Cirsium palustre</i>	3.59	1.55	0.90	2.00	0.153	Shallow striate	Pappus	89.83	0.149	Persistent
<i>Cirsium rivulare</i>	4.02	1.54	0.77	2.40	0.178	Fine striate with ribs	Pappus	91.84	0.119	Persistent
<i>Crepis paludosa</i>	4.80	0.60	0.45	0.69	0.265	Longitudinal furrows	Pappus	84.99	0.234	Transient
<i>Filipendula ulmaria</i>	4.20	1.90	0.45	0.99	0.203	Glabrous		86.24	0.210	Transient
<i>Galium uliginosum</i>	1.20	0.85		0.29		Granulate				
<i>Geum rivale</i>	10.50	1.35	0.60	1.22	0.275	Dull with long glandulars and short glandular hairs	Hairs	89.17	0.169	Transient
<i>Juncus effusus</i>	0.52	0.23	0.20	0.01	0.115	Longitudinal ribbed and transversal ringed		51.17	0.754	Persistent
<i>Lotus uliginosus</i>	1.13	1.00	1.00	0.40	0.004	Smooth		60.94	0.544	Persistent
<i>Luzula luzuloides</i>	1.44	0.72	0.68	0.30	0.088	Faint longitudinal striated		73.81	0.392	Persistent
<i>Lychnis flos-cuculi</i>	0.88	0.75	0.50	0.21	0.048	Covered with closely-spaced, stelliform papillae, margin prickly		68.38	0.468	Persistent
<i>Lycopus europaeus</i>	1.50	1.25	0.65	0.28	0.085	Fine wrinkly		73.16	0.402	Persistent
<i>Lysimachia vulgaris</i>	1.20	1.20	0.65	0.30	0.070	Fine foveolate		72.71	0.406	Persistent
<i>Lythrum salicaria</i>	1.15	0.50	0.29	0.06	0.152	Reticulate		65.12	0.538	Persistent
<i>Mentha longifolia</i>	0.66	0.40	0.34	0.12	0.066	Reticulate		65.98	0.511	Persistent
<i>Myosotis palustris</i>	1.55	1.05	0.50	0.35	0.114	Smooth		76.16	0.360	
<i>Peucedanum palustre</i>	4.69	3.46	0.66	2.70	0.194	Smooth		93.08	0.101	Transient

Species	Length (mm)	Width (mm)	Height (mm)	Weight (mg)	Shape index (VS)	Surface texture	Appendages	Depth distribution index (D)	Longevity index (L)	Persistence*
<i>Potentilla erecta</i>	1.55	1.05	0.90	0.58	0.048	Glabrous, rugose-ribbed and often sparse tuberculate		77.53	0.355	Persistent
<i>Scutellaria galericulata</i>	1.48	1.28	1.02	0.70	0.024	Dense verrucose		73.51	0.375	Persistent

*According to Thompson et al. [25].

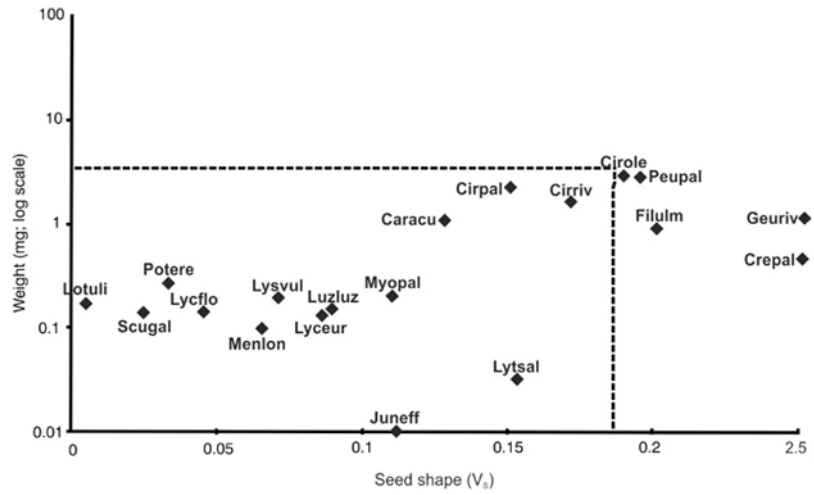


Fig. 2 Relationship between seed weight and shape (variance of seed dimension in species identified on necromass). The dotted line encloses the region within all propagules are long lived and formed persistent seed bank.

on the necromass sampled in late fall would be higher than that obtained in the samples collected in spring. However, the methodology employed in this study seems to be justified, since it is assumed that most seeds should enter the soil seed bank at the beginning of the growing season, while seeds remaining on the necromass form its own bank.

Necromass is formed primarily by ramets of *Carex acutiformis*, a species present in all the analyzed vegetation patches due to its highly effective vegetative reproduction. Similar results were reported by Borkowska [18,19] in investigations conducted on abandoned meadows in the Narewka River valley, Białowieża National Park (NE Poland). Accumulation of large amounts of necromass produced by this species reduces the spread of other taxa. Another sedge species, *C. cespitosa*, exhibits similar competitive abilities. Initially, individuals of meadow species can grow freely between its tussocks only to be eliminated later by the sedge shoot necromass. In turn, *C. cespitosa* tussocks become a suitable environment for many herbaceous species whose growth has been previously limited by necromass accumulated around the tussocks [41,42]. Kostrakiewicz-Gieralt [43] noted the presence of seedlings of 64 taxa in *Deschampsia caespitosa* tussocks. In small tussocks anemochorous and hydrochorous taxa dominated, the frequency of endo- and epizoochorous taxa was much lower, while the percentage of species characterized by other modes of diaspore dispersal attained the lowest rates. In large tussocks, anemochorous and epizoochorous species prevailed, the share of endozoochorous and hydrochorous taxa was lower, and the contribution of species characterized by other modes of dissemination was very scarce.

The layer of dead plant matter forms a physical barrier to falling seeds. Approximately between 300–400 (Patches A, B, and D) and nearly 5000 (Patch C) seedlings m⁻² representing 21 taxa emerged on the material sampled from the study area. Similar results were obtained by Borkowska [19], who identified 237 seedlings from 11 taxa, dominated by *Lythrum salicaria*, *Epilobium* sp., and *Lysimachia vulgaris*, on the same surface area in 1-year investigations of seed germination in greenhouse conditions. A 2-fold higher number of seedlings emerged on the necromass with a high degree of decomposition, in comparison with the seedling number noted on the non-decomposed material. Only one of the taxa identified in the necromass sampled from the macroforb meadows in the Szum River valley was absent in the plant cover. This was *Luzula luzuloides*, whose seeds probably originate from a population inhabiting the hornbeam-oak forest situated on the left slope of the valley below the complex of the meadow communities [28] (also, Czarnecka, unpublished). The study of

the structure of the soil seed bank in the analyzed vegetation patches conducted by Franczak and Czarnecka [44] showed bank resources at a level of ca. 3800 seeds m⁻². This indicates that the number of seeds that germinated on the necromass accounts for minimum 10% of the soil seed bank or, in some cases, may be even higher. Under field conditions, the authors observed single seedlings on partly decomposed necromass. No presence of seedlings was noted on new residual plant material. In an experiment conducted in a similar system of plant communities, Borkowska [19] showed that removal of the vegetation cover, including necromass, increased the number of meadow species and the density of their seedlings. This treatment was regarded as a disturbance, which under natural conditions may occur as a result of, e.g., foraging on the aboveground plant parts by herbivores or ground rooting by wild boars [45–48]. In meadow vegetation patches analyzed in various stages of succession, Borkowska [19] found that the formed gaps served as safe germination sites [40] or regeneration niches *sensu* Grubb [49]. However, this condition did not persist long. Already after 4 years, the gaps formed by the removal of the vegetation were colonized, primarily by species with a vegetative propagation mode (mainly *C. acutiformis*). These investigations were continued in the aspect of the dynamics of *Cirsium rivulare* populations in a meadow that had undergone succession [50]. Experimental vegetation gaps were created in patches dominated by various species to determine the effect of necromass on the presence of *C. rivulare* seedlings. A considerable rise in the number of seedlings of this species was noted in patches dominated by *C. acutiformis* and *F. ulmaria*, following necromass removal in comparison with plots containing necromass.

Formation of gaps by fallen trees and ground rooting by wild boars in a dense vegetation cover also affected the abundance of a *Senecio rivularis* population [51,52]. Disturbance of this kind has a positive effect on the intensity of germination, rate of appearance and survivorship of seedlings from the current year seeds (appearing in openings formed in early summer) as well as of those from the previous year deposited in soil, i.e., germinating in the gaps formed in early spring. This was also confirmed by previous results reported by Falińska [53,54], who found that the accumulated necromass inhibited seedling recruitment and lowers the rate of species exchange during succession. In the case of *Cirsium palustre* populations, the removal of the vegetation cover was followed by a considerable increase in the number of seedlings [55]. Similarly, investigations of an annual halophyte species *Salicornia patula* show that necromass is one of the limiting factors in development of the plant in salt pans. An increase in the necromass thickness accompanied the succession process. The mosaic structure of the habitat increased, which simultaneously contributed to a decline in the *S. patula* population [56]. In investigations of *Iris sibirica* populations, Kostrakiewicz [57] noted the presence of seedlings of this species mainly in sites that were devoid of a dense vegetation cover and served as gaps. The author reported similar results in her analysis of *Trollius europaeus* populations. Based on the results, the author concluded that formation of gaps seemed to be a very effective way of active protection of endangered populations [58] and that heterogenous microsite conditions in openings facilitated recruitment of taxa with various germination requirements and contributed to the maintenance of species diversity [59].

A dense vegetation cover limits seedling recruitment also in forest habitats. An experiment conducted by Pirożnikow [60] in a natural deciduous forest habitat in the Białowieża National Park (NE Poland) showed that removal of the vegetation cover favored the development of seedlings of many species, which would have had no chance of survival in dense ground layer. Seedlings of 48 species were noted in plots where the plant cover had been removed, while seedlings of only 17 species were found in intact plots. Necromass also limits recruitment of new individuals in coniferous woods [61]. In this case, the needle layer did not prevent seeds from reaching the soil but strongly reduced seedling emergence from the seed bank. Removal of necromass may be a recommended technique to accelerate natural restoration in pine plantations. Dzwonko and Gawroński [62] reported that small seeded species (mass ≤10.0 mg) are mostly affected by the presence of needles, as they lack nutrient reserves to grow across the mechanical barrier imposed by the litter. The seeds with mass larger than 10.0 mg have a greater ability to germinate under litter. Such seedlings may penetrate the litter as a result of rapid and extensive initial growth of the shoot and root using a comparatively large amount of seed reserves.

According to Xiong et al. [63], seed germination and establishment of new individuals were more negatively affected by litter in trees than in forbs and grasses. This statement is in contrast to the assumption that their larger seeds and taller seedlings will make trees more tolerant to litter. Kostel-Hughes et al. [64] have found that smaller-seeded species (*Betula lenta* and *Liquidambar styraciflua*) have reduced germination with litter depth increasing while larger-seeded species (*Quercus* spp.) were usually unaffected or increased by leaf litter. Larger seeds may be less susceptible to certain physical conditions, such as shade or leaf litter, because of greater energy reserves. The authors have also suggested that larger-seeded species can establish and grow under a wider range of physical conditions than smaller-seeded species. However, some studies suggest that large-seeded species are more affected by litter chemistry than small-seeded ones [65] and that larger seeds may be easily attacked by pathogens and predators attracted to litter [8,15].

Two forb species, *L. vulgaris* and *L. salicaria*, dominating the necromass, in the soil seed bank and vegetation cover [44]. *Juncus effusus* was the third taxon represented abundantly in the necromass and the soil seed bank, whereas its low cover was noted in the plant cover. *Lythrum salicaria* and *J. effusus* seeds are characterized by the lowest weight among all the identified propagules and small sizes, which promotes capture thereof in the necromass layer. Additionally, these taxa produce a substantial number of highly viable seeds and form a persistent seed bank [66–69]. The germination of fresh *L. salicaria* seeds may reach up to 100% and declines in 2–3-year-old seeds to approximately 80% (Franczak, unpublished). Welling and Becker [70] estimated that as many as 410 000 seed of the purple loosestrife might be present on 1 m² of soil to a depth of 5 cm. Seeds with a large size and weight reach the soil surface easily, penetrating the necromass barrier.

Conclusions

- The necromass is an effective reservoir of meadow species, which may contribute to depletion of the resources of the soil seeds bank.
- The seeds have an ability to germinate on the necromass.
- The investigations show that the seeds of the taxa present on the necromass having the largest sizes (e.g., *Cirsium* spp., *Geum rivale*), are elongated and flattened (the highest values of the shape index) and are equipped with additional elements such as pappus or hairs, which help them to remain on dead plant shoots.
- A majority of the species present on the necromass is able to form a persistent seed bank, which is indicated by the low values of diaspore weight (<3 mg) and shape index ($V_s < 0.18$).

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Nekromasa jako rezerwuarnasion w zbiorowiskach zmiennowilgotnych łąk ziołoroślowych

Streszczenie

Nekromasa, czyli obumarłe części roślin, wywiera duży wpływ na kształtowanie się wzorców przestrzennych populacji i zbiorowisk. W zależności od miąższości i stopnia dekompozycji może stanowić barierę fizyczną blokującą przestrzeń i utrudniającą rekrutację osobników, także na drodze autotoksykacji. Celem badań było określenie roli warstwy nekromasy w kształtowaniu się zasobów glebowego banku nasion zmiennowilgotnych łąk ziołoroślowych oraz jej wpływu na efektywność reprodukcji generatywnej. Autorki szczególną uwagę zwróciły na możliwość przechwytywania i zatrzymywania przez nekromasę nasion gatunków występujących w pokrywie roślinnej.

W pokrywie roślinnej zidentyfikowano w sumie 52 gatunki roślin naczyniowych. Na nekromasie pojawiło się, w zależności od płatu, od 10 do 13 taksonów. Zagęszczenie siewek wahało się w granicach od 339 do 4923 m⁻². Gatunkami, których siewki dominowały we wszystkich płatach były *Lythrum salicaria* i *Lysimachia vulgaris*. Te dwa gatunki charakteryzowały się także najwyższą frekwencją. Niskie wartości wskaźnika Jaccarda (0.28–0.36) wskazują na niewielki udział gatunków wspólnych dla nekromasy i pokrywy roślinnej. Taki wynik można tłumaczyć występowaniem dużych dysproporcji w liczbie wszystkich taksonów oznaczonych na nekromasie i w pokrywie roślinnej. Nasiona z reguły charakteryzują się niewielkimi rozmiarami i w większości posiadają gładką powierzchnię lub są delikatnie prążkowane i/lub żebrowane. U nasion największych i najcięższych taksonów (*Crepis paludosa*, *Geum rivale* i *Cirsium* spp.) obecność dodatkowych struktur, takich jak *pappus* i włoski, może sprzyjać zatrzymywaniu się ich na nekromasie.