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Effect of expansive species on seed rain and soil seed bank of mountain mesic meadows

Auswirkungen sich ausbreitender Arten auf den Sameneintrag und die Samenbank in mäßig nährstoffreichen Bergwiesen

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Abstract

The degradation of species-rich mountain meadows has been observed in many parts of Central Europe in the last few decades. It is reflected in decreasing species numbers and changes in the proportions of plant species in the aboveground vegetation. Some species are increasing in abundance and eventually dominate the meadow vegetation. There is still a lack of studies explaining how this process is reflected in the soil seed bank. Therefore, the goal of the current study was to test whether expansive species that degrade aboveground vegetation of mountain meadows also influence, quantitatively and qualitatively, seed rain and seed bank. Soil samples were taken from 14 plots in degraded patches and another 14 plots in non-degraded patches. Nearly the same numbers of seedlings were recorded in both meadow types. In both cases, low similarities between aboveground vegetation and soil seed rain and seed bank were observed. Expansive species causing meadow degradation (*Calamagrostis epigejos*, *Festuca rubra*, *Deschampsia cespitosa* and *Lupinus polyphyllus*) reached cover values of 60–83% in the aboveground vegetation, and a share of up to 36% in the seed rain and seed bank. The mean species richness in the aboveground vegetation and the soil of degraded meadows was lower than in the non-degraded plots. However, the seed bank may buffer degradation to some extent since the degradation of aboveground vegetation was faster than impoverishment of seed bank. Consequently, seed rain and seed bank of degraded meadows still contained typical mesic meadow species in similar proportions as non-degraded meadows. This indicates that seed rain and seed bank may contribute to the restoration of degraded meadows after the removal of expansive species from the aboveground vegetation.

Keywords: *Arrhenatheretalia*, degradation of vegetation, grassland, Polish Sudetes Mts, species richness

Erweiterte deutsche Zusammenfassung am Ende des Artikels

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1. Introduction

Degradation of grassland plant communities is a common phenomenon in Europe (e.g. PRACH 2008, HOOFTMAN & BULLOCK 2012, METSOJA et al. 2014, PRUCHNIEWICZ & ŻOŁNIERZ 2014). This phenomenon results in the reduction, or even severe decline, of species diversity in formerly species-rich meadows (KRAUSE et al. 2011, WESCHE et al. 2012). Either management intensification or the abandonment of grasslands may be the causes of this decline (WAESCH & BECKER 2009, PARTZSCH 2011, KRAUSE & CULMSEE 2013). Grassland abandonment is common in mountain areas and leads to a decrease in species diversity of meadows and pastures, which are considered to be among the most species-rich semi-natural plant communities (e.g. NIEDRIST et al. 2009, SCOTTON et al. 2009, PAVLŮ et al. 2011, DENGLER et al. 2014).

The decrease in species diversity is also a concern in the grasslands of the Sudetes Mts. (KRAHULEC et al. 1996, HANDLOVÁ & MÜNZBERGEROVÁ 2006, PAVLŮ et al. 2011, PRUCHNIEWICZ & ŻOŁNIERZ 2014), which is a medium altitude Hercynian range shared between Poland and the Czech Republic. In the Polish part of the Sudetes Mts., the most important reason for grassland degradation is the cessation of management, which has increased during the past 25 years due to economic reasons. Degradation of the abandoned mesic Sudetian grasslands is usually connected to changes in the original proportions of species, notably the increasing dominance of a few species and an overall decrease in species diversity. Grasses, including *Calamagrostis epigejos*, *Festuca rubra* and, less frequently, *Deschampsia cespitosa,* are the most expanding species dominating swards of abandoned mesic mountain grasslands (PRUCHNIEWICZ & ŻOŁNIERZ 2014). *Calamagrostis epigejos* as a strongly competitive species, which produces particularly dense and thick litter and prevents the germination of other species (REBELE 2000, SEDLÁKOVÁ & FIALA 2001), may degrade various plant communities (REBELE & LEHMANN 2001). Vegetation dominated by *F. rubra* and *D. cespitosa* is a frequent phenomenon in the Sudetes Mts. (PRUCHNIEWICZ & ŻOŁNIERZ 2014), with similar effects as the dominance of *F. rubra* in calcareous grassland in Belgium (JACQUEMYN et al. 2011).

A fast-progressing degradation and decline in the biodiversity of mountain grasslands raises an urgent need for their restoration (e.g. KRAHULEC et al. 2001, HÁZI et al. 2011, PRUCHNIEWICZ & ŻOŁNIERZ 2014). The prerequisite for developing proper measures for active conservation of these communities is the comprehensive understanding of processes leading to degradation under various regional and local conditions. Additionally, the natural regeneration potential of these plant communities needs to be quantified. In this context, the soil seed bank may play an important role in the recovery of species composition in restored grassland (e.g. LÓPEZ-MARIÑO et al. 2000, BOSSUYT & HONNAY 2008, RUPRECHT et al. 2010). There are some controversies about the significance of the soil seed bank for grassland restoration. Some authors believe that it may be important to obtain the proper species composition of meadows (BAKKER & BERENDSE 1999, KALAMEES et al. 2012, METSOJA et al. 2014). Other studies indicate that restoration cannot be based only on the persistent seed bank, as it is an insufficient source of the species needed to recreate a species-rich plant community (BOSSUYT & HERMY 2003, BOSSUYT & HONNAY 2008, TÓTH & HÜSE 2013). In this case an active introduction of seeds of target species will be necessary to obtain a species composition in restored grasslands that matches that of target communities (DONATH et al. 2007, KIEHL et al. 2010, SCHMIEDE et al. 2012, PLUE & COUSINS 2013, METSOJA et al. 2014).

A number of studies were published in the last decade concerning the influence of management history, its intensity or cessation on the soil seed bank (e.g. WELLSTEIN et al. 2007, JACQUEMYN et al. 2011, AUESTAD et al. 2013). While soil seed banks are well studied in dry calcareous grasslands (WILLEMS & BIK 1998, BOSSUYT et al. 2006, VALKÓ et al. 2011), the properties of soil seed rain and seed banks of mesic *Arrhenatheretalia* grasslands are still far less known. Therefore, in the current paper we addressed the following main question: What is the effect of the degradation of mesic grasslands caused by the strong dominance of expansive species on the properties of the soil seed rain and seed bank? We tested the hypothesis that degraded and species-rich non-degraded meadows differ both quantitatively (species richness, seed numbers) and qualitatively (species composition) with respect to their seed rain and seed bank. We also tried to evaluate whether the seed bank of degraded meadows may be used during their restoration as a source of future species diversity.

More specifically, the objective of our study was to answer the following questions: (1) Are differences in aboveground species richness between non-degraded and degraded meadows of the Sudetes Mts. reflected in their seed rain and seed bank? (2) To which degree is the species composition of the aboveground vegetation similar to that of the seed rain and seed bank in both types of meadows? (3) Does the seed rain and seed bank of degraded grasslands still contain seeds of species of the non-degraded meadows, which could support the restoration of mountain meadows?

2. Material and methods

2.1 Study sites

The study was conducted on mesic meadows in the Polish parts of the Central Sudetes (N 50°36'39''–50°39'35''; E 16°25'56''–16°31'26''; altitude 410–860 m, slope inclination 2–10°). This region is characterised by a moderate climate, with a mean annual temperature around 7 °C and an average annual precipitation of about 650 mm.

2.2 Sampling design

Data collected from 100 plots in a previous study (PRUCHNIEWICZ & ŻOŁNIERZ 2014) were used to select 28 research plots (5 m x 5 m) for the investigation of the soil seed bank. Fourteen of these plots represented regularly managed, species-rich meadows, which are referred to as non-degraded meadows from here on. The vegetation of these grasslands still contains typical meadow species. In the category 'typical meadow species', we include diagnostic species for the alliances *Arrhenatherion elatioris* W. Koch 1926, *Polygono-Trisetion* Br.-Bl. et Tx. ex Marschall 1947 nom. invers. and *Cynosurion cristati* Tx. 1947 belonging to the *Arrhenatheretalia* Tx. 1931 order according to HÁJKOVÁ et al. (2010), which are frequent in non-degraded meadows in the area. Before the study started, farmers were interviewed with a set of questions concerning the history of their meadows and ways of management. According to the information obtained from farmers, regular management in the area consists of mowing once a year, with usually no or sporadically very low fertilization. Only meadows unfertilized for at least three years and mown not earlier than in second half of June were chosen for the study. Another independent set of 14 plots was established within large patches of degraded meadows which were abandoned or have been irregularly used within the last decade. None of the sampled meadows originated from arable land. Plots in degraded meadows were established in the central parts of patches dominated by competitively dominant species, not closer than 50 m from their edges. The vegetation of these meadows was strongly dominated by *Calamagrostis epigejos* (7 plots, 82.9% average cover), *Festuca rubra* (2 plots, 80% average cover), *Deschampsia cespitosa* (4 plots, 67.5% average cover) or *Lupinus polyphyllus* (1 plot, 60% cover). The minimum distance between plots representing degraded and non-degraded meadows was about 100 meters. Vegetation was sampled on each plot in the first half of July. The species cover was expressed on a percentage scale. Seven soil subsamples were randomly collected from each study plot in the second half of August using a sampler with a diameter of 8 cm and a height of 10 cm. After removing runners and roots, the soil samples were divided into three layers: 0–1 cm to extract information on seed rain, and 1–5 cm and 5–10 cm, which together contain two fractions of the seed bank. For each layer, all 7 subsamples were then combined into one sample. In the laboratory, the soil samples were dried for one month at room temperature in the dark.

2.3 Seed bank analysis

The analysis of the seed bank was conducted at the Justus Liebig University in Giessen, IFZ (Germany) in a greenhouse with controlled temperature (Tmin ~14°C, Tmax ~23°C), light (6:00–22:00, h ~10 klx), humidity (~70%) and automatic watering (twice daily). For the assessment of the seed bank, we used the emergence method (ROBERTS 1981), which is based on the direct germination of seeds from the soil. Soil samples were filled up in 18 cm × 28 cm × 2 cm styrofoam trays. The experiment included a total of 84 trays (28 research plots × 3 layers). The germination started about 1 week after the beginning of the experiment. Species that could not be identified immediately at the seedling stage were transplanted into separate pots for later identification. Except for *Carex* spp., all plants were recognized at the species level. After 3 months, when germination ceased pots were allowed to air dry for two weeks, whereupon the soil was carefully stirred and the pots were incubated for another 3 months.

2.4 Statistical analyses

Normal distribution of data was checked by the Shapiro–Wilk's test. Variables consistent with a normal distribution were tested by parametric methods: Pearson correlation (r) or Student's t-test. Data lacking normal distribution were tested using non-parametric methods: Spearman rank correlation (r_s), Wilcoxon signed rank test for paired data and Mann–Whitney U test. All statistical analyses were performed using STATISTICA v. 12 software (STATSOFT INC. 2014).

In order to compare the species composition of the aboveground vegetation and its seed rain and seed bank a non-metric multidimensional scaling (NMDS) with Bray-Curtis distance measure was used. To determine the number of dimensions for each NMDS, stress values were assessed (MCCUNE & GRACE 2002). In order to reduce the stress values below 20%, we decided to use a 3-dimensional solution. The data were log-transformed. The calculations were performed using the program CANOCO v. 5.03 (TER BRAAK & ŠMILAUER 2012).

The diversity of the vegetation and the seed rain and seed bank was assessed by the species richness and diversity indices for each study plot. The Shannon diversity index was calculated as: $H' = -\Sigma (p_i * \ln p_i)$, and the evenness index was calculated as: $J' = H'/\ln S$, where $p_i = n_i/N$; n_i = the abundance of the i^{th} species expressed as its cover; N = the sum of abundances of all species, and S = the total species richness. The MVSP v. 3.131 package (KOVACH 2007) was used to calculate all diversity indices.

The similarity between the aboveground vegetation and the seed rain and seed bank was compared using the Jaccard similarity coefficient (ŠMILAUER & LEPŠ 2014).

3. Results

3.1 Aboveground vegetation

The non-degraded meadows were characterized by a high average species richness (±SE) per 25 m^2 plot of 25.6 ± 1.71, and a species composition typical for the *Arrhenatheretalia* order. Analysis of functional groups in the aboveground vegetation of the non-degraded meadows indicated a higher proportion of forb species (67.4%) than of grasses (28.8%). Trees in the herb layer (saplings) accounted for 3.8% of species.

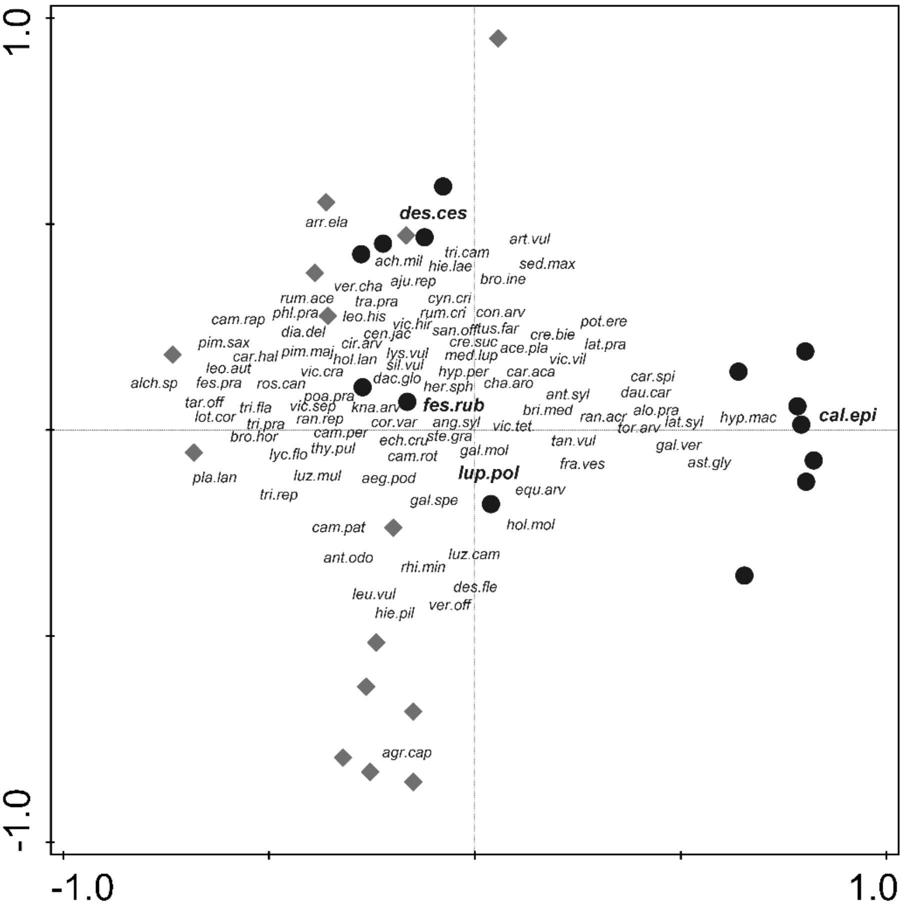

Fig. 1. Non-metric multidimensional scaling (NMDS) ordination plot for the aboveground vegetation of the degraded (filled circles) and non-degraded (gray diamonds) meadows. Abbreviations of species names are found in Supplement E1.

Abb. 1. NMDS-Ordinationsdiagramm der oberirdischen Vegetation von degenerierten (gefüllte Kreise) und nicht degenerierten Wiesen (graue Quadrate). Für Abkürzungen der Artnamen, siehe Anhang E1.

In the case of degraded meadows, the aboveground vegetation was dominated by *Calamagrostis epigejos*, *Festuca rubra*, *Deschampsia cespitosa* or *Lupinus polyphyllus*. The average species richness of these plots (15.71 ± 1.83) was significantly lower than that of non-degraded meadows ($t_{26} = -3.96$; $p < 0.001$). Significant differences between the degraded (D) and non-degraded meadows (ND) were also found for the Shannon diversity index ($H'_D = 1.58 \pm 0.13$; $H'_{ND} = 2.04 \pm 0.14$; $t_{26} = -2.35$; $p = 0.027$), but not for the evenness index ($J'_D = 0.58 \pm 0.03$; $J'_{ND} = 0.63 \pm 0.04$; $t_{26} = -0.94$; $p = 0.35$). In the aboveground vegetation of degraded meadows, the proportion of herb species (64.1%) was higher than the proportion of grass species (35%). Tree seedlings in the herb layer accounted for 0.9% of species.

In the non-metric multidimensional scaling (NMDS) of the aboveground vegetation the eigenvalues for the first two axes were 0.43 and 0.34, respectively. The cumulative values of the explained variance of species data for those axes were 43.0% and 77.0%, respectively. The stress value reached an acceptable level of 15.2. Centroids of plots for degraded and non-degraded meadows were separated in the ordination space, demonstrating large differences in vegetation composition. The degraded meadows were grouped according to the dominant expanding species in the aboveground vegetation. While plots dominated by *C. epigejos* were placed on the right hand side of the first axis (r_{axis1} = 0.936), plots dominated by *F rubra* (r_{axis1} = -0.273), and the one dominated by *L. polyphyllus* (r_{axis1} = 0.038) was placed in the middle of the first axis. Plots with *D. cespitosa*, a species of irregularly managed meadows, were placed at the lower part of the second axis (r_{axis2} = 0.526) (Fig. 1).

3.2 Seed rain and seed bank

In total, 7,209 seedlings were recorded, of which 3,591 were found in soil samples taken from degraded meadows and 3,618 in samples from non-degraded grasslands. In the seed rain and the seed bank of degraded meadows, the following species were most frequent: *Hypericum maculatum* (Σ = 1,467 seedlings), *Agrostis capillaris* (Σ = 598 seedlings), *C. epigejos* (Σ = 381 seedlings) and *F. rubra* (Σ = 381 seedlings). For the non-degraded meadows, the largest numbers of seedlings were noted for *A. capillaris* (Σ = 914 seedlings), *H. maculatum* (Σ = 787 seedlings), *Arrhenatherum elatius* (Σ = 481 seedlings), *F. rubra* (Σ = 345 seedlings), and *Veronica chamaedrys* (Σ = 139 seedlings).

In both categories of meadows, the highest seed numbers occurred in the 0–1 cm seed rain layer (Table 1). There were also differences in the seed density between corresponding soil layers in both categories of meadows; however, they turned out to be non-significant (Mann-Whitney U test).

The highest species richness was found in the 1–5 cm layer, and the lowest was noted in the deepest layer. Comparing degraded and non-degraded meadows, significant differences were found only for the species richness in the 5–10 cm layer (Z = -2.37; p = 0.02), the Shannon diversity index calculated for 1–5 cm (Z = -3.01; p = 0.026), 5–10 cm depth (t_{26} = -3.78; $p < 0.001$) and evenness calculated for 5–10 cm depth (t_{26} = -2.14; p = 0.04; Fig. 2).

Table 1. Number of seeds per plot and per cm soil depth in different soil layers of degraded and non-degraded meadows. Different superscript letters denote significant differences between layers within each category of meadows according to Wilcoxon signed rank test.

Tabelle 1. Anzahl der Samen pro Plot und cm Bodentiefe in unterschiedlichen Bodenschichten degenerierter und nicht degenerierter Wiesen. Unterschiedliche hochgestellte Buchstaben kennzeichnen für den jeweiligen Wiesentyp statistisch signifikante Unterschiede nach dem Wilcoxon Vorzeichen-Rang Test.

	Degraded meadows			Non-degraded meadows		
Layer [cm]	0–1	1–5	5–10	0–1	1–5	5–10
mean	75.21^{a}	24.23^{b}	12.03^{b}	88.36^{a}	21.87^{b}	12.14^{b}
± SE	16.29	4.78	3.10	18.69	4.85	2.75
minimum	15	5	0	7	2	2
maximum	262	74	48	232	59	39

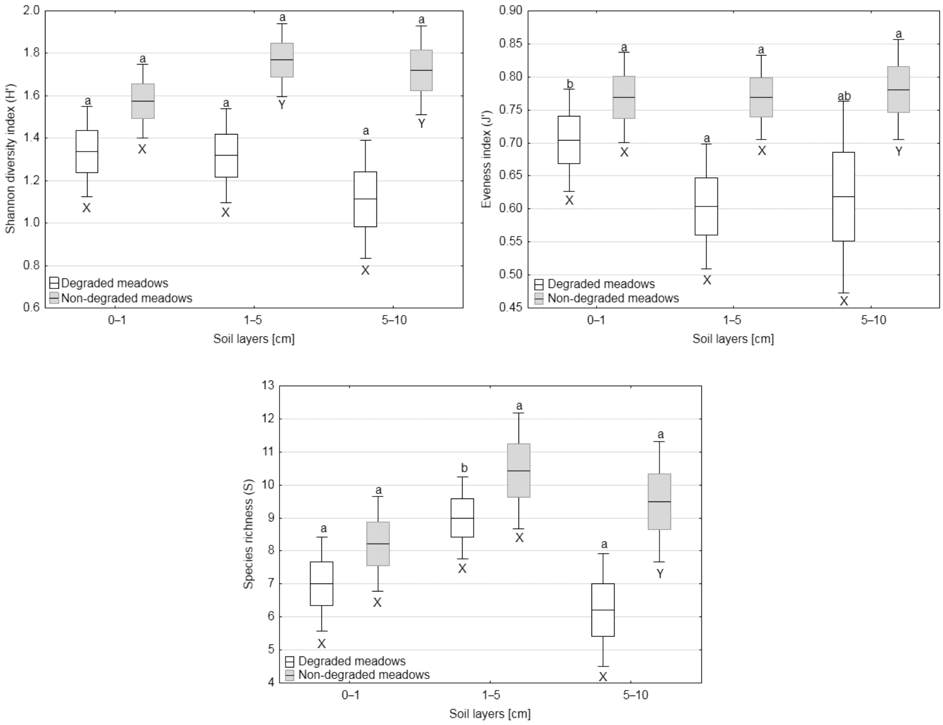

Fig. 2. Shannon diversity index (H'), evenness index (J') and species richness (S) of the seed rain (0–1 cm) and two seed bank layers (1–5 cm, 5–10 cm) of degraded and non-degraded meadows. Box plots give means (horizontal lines), standard error (boxes) and confidence intervals (whiskers). Different lowercase letters (a, b) indicate significant differences between different soil layers within each meadow type according to Wilcoxon signed rank test. Different uppercase letters (X, Y) denote significant differences between degraded and non-degraded meadows within each soil layer according to Student's t-test or Mann–Whitney U test.

Abb. 2. Shannon Diversität (H'), Evenness (J') und Artenreichtum (S) von Samenregen (0–1 cm) und zwei Samenbankschichten (1–5 cm, 5–10 cm) in degenerierten und nicht degenerierten Wiesen. In den Box-Whisker-Plots sind der Mittelwert (horizontale Linie), der Standardfehler (Kasten) und das Konfidenzintervall (Whisker) dargestellt. Unterschiedliche Kleinbuchstaben (a, b) kennzeichnen signifikante Unterschiede zwischen verschiedenen Bodenschichten innerhalb jeden Wiesentyps nach Wilcoxon Vorzeichen-Rang Test. Unterschiedliche Großbuchstaben (X,Y) kennzeichnen signifikante Unterschiede zwischen degradierten und nicht-degradierten Wiesen innerhalb jeder Bodenschicht nach Student's t-Test oder Mann–Whitney U Test.

To examine the variation in species composition of the seed bank during the degradation process, non-metric multidimensional scaling (NMDS) was used (Fig. 3). The eigenvalues for the first two axes were 0.40 and 0.35, respectively. The cumulative values of the explained variance of species data for the first two axes were 40.4% and 75.2%, respectively. The stress value was 15.1. Non-degraded and degraded meadows were placed within the NMDS ordination space at the opposite ends of the first and second axis. Typical mesic meadow species were mainly gathered in the right part of the diagram, within the middle along the second axis. Species indicative for meadow degradation, i.e., *C. epigejos*

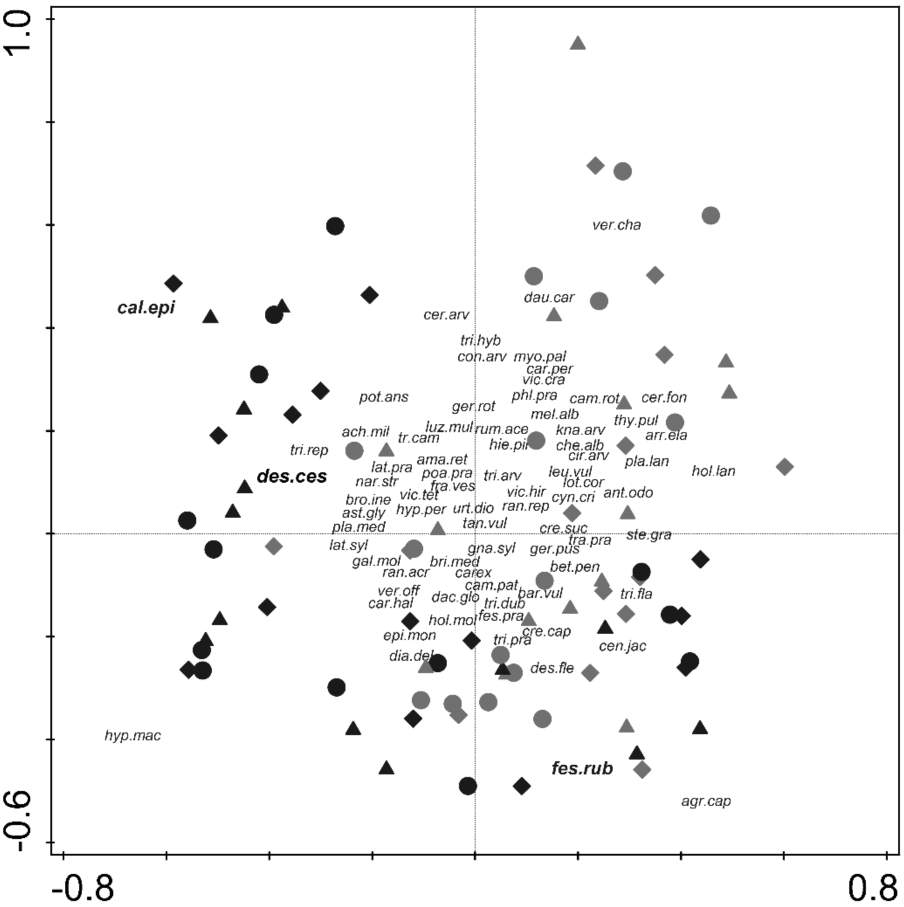

Fig. 3. Non-metric multidimensional scaling (NMDS) ordination plot for the seed bank of degraded and non-degraded meadows. The black symbols represent degraded meadows, the gray symbols represent non-degraded meadows. The seed rain is marked as diamonds, the layer 1–5 cm as circles, and the 5–10 cm layer as triangles. For abbreviations of species names see Supplement E1.

Abb. 3. NMDS-Ordination der Samenbanken degenerierter (schwarze Symbole) und nicht degenerierter Wiesen (graue Symbole) differenziert nach Samenregen (Quadrate), der Schicht 1–5 cm (Kreise) und der Schicht 5–10 cm (Dreiecke). Für Abkürzungen der Artnamen, siehe Ahang E1.

(r_{axis1} = -0.640; r_{axis2} = 0.411) and *D. cespitosa* (r_{axis1} = -0.185; r_{axis2} = 0.130) were placed on the left hand side of the diagram and in the centre along the 2[nd] axis. *Festuca rubra* (r_{axis1} = 0.154; r_{axis2} = -0.589), which was less abundant in the non-degraded vegetation, was placed at the lower part of the second axis. This indicator for degraded grasslands was more abundant in the seed rain than in the seed bank.

In degraded grasslands typical meadow species, such as *A. capillaris*, *A. elatius*, *Plantago lanceolata* and *Vicia cracca*, still had seeds in the deeper layers of the soil in proportions similar to those observed in non-degraded meadows (Table 2).

Table 2. Frequency (%) of typical meadow species and expansive species (marked with *) in the aboveground vegetation (Veg.), seed rain (0–1 cm) and seed bank (1–5 cm, 5–10 cm) of degraded and non-degraded grasslands.

Tabelle 2. Prozentuale Häufigkeit typischer Wiesenarten und expansiver Arten (mit * gekennzeichnet) in der oberirdischen Vegetation (Veg.), dem Samenregen (0–1 cm) und der Samenbank (1–5 cm, 5–10 cm) degenerierter und nicht degenerierter Wiesen.

Species	Degraded meadows				Non-degraded meadows			
	Veg.	0–1	1–5	5–10	Veg.	0–1	1–5	5–10
Achillea millefolium	64.3	7.1	21.4	14.3	85.7	21.4	28.6	28.6
Agrostis capillaris	21.4	50.0	64.3	42.9	64.3	78.6	71.4	57.1
Alchemilla sp.	28.6	.	.	.	64.3	.	.	.
Alopecurus pratensis	7.1	.	.	.	.	.	.	.
Anthoxanthum odoratum	35.7	21.4	21.4	7.1	92.9	28.6	50.0	42.9
Arrhenatherum elatius	57.1	50.0	57.1	42.9	85.7	64.3	64.3	71.4
*Calamagrostis epigejos**	50.0	50.0	50.0	50.0	7.1	.	.	.
Campanula patula	14.3	7.1	.	.	28.6	.	7.1	7.1
Campanula rotundifolia	28.6	.	.	.	28.6	.	7.1	14.3
Cardaminopsis halleri	.	.	.	.	14.3	.	7.1	.
Carlina acaulis	14.3	.	.	.	7.1	.	.	.
Centaurea jacea	14.3	7.1	7.1	7.1	7.1	.	.	.
Cynosurus cristatus	7.1	.	.	.	14.3	7.1	.	7.1
Dactylis glomerata	71.4	42.9	64.3	42.9	64.3	35.7	50.0	42.9
*Deschampsia cespitosa**	57.1	14.3	7.1	7.1	42.9	.	.	.
Festuca pratensis	14.3	7.1	14.3	7.1	42.9	7.1	.	.
Festuca rubra *	78.6	57.1	64.3	78.6	78.6	71.4	57.1	57.1
Galium mollugo	78.6	7.1	28.6	.	71.4	.	7.1	.
Holcus lanatus	28.6	7.1	42.9	7.1	57.1	42.9	28.6	21.4
Hypericum maculatum	71.4	71.4	78.6	71.4	71.4	71.4	78.6	71.4
Knautia arvensis	14.3	.	.	.	57.1	.	7.1	.
Leontodon autumnalis	7.1	.	.	.	14.3	.	.	.
Leontodon hispidus	7.1	.	.	.	7.1	.	.	.
Leucanthemum vulgare	.	.	7.1	.	21.4	.	14.3	14.3
Lotus corniculatus	28.6	.	7.1	.	78.6	.	7.1	7.1
*Lupinus polyphyllus**	14.3	.	.	.	.	.	.	.
Pimpinella saxifraga	14.3	.	.	.	57.1	.	.	.
Plantago lanceolata	21.4	.	14.3	.	57.1	28.6	35.7	14.3
Poa pratensis	21.4	7.1	.	7.1	42.9	.	7.1	14.3
Rumex acetosa	35.7	7.1	.	7.1	71.4	7.1	7.1	42.9
Stellaria graminea	35.7	42.9	28.6	7.1	57.1	50.0	42.9	42.9
Tragopogon pratensis	21.4	7.1	.	.	50.0	.	.	.
Trifolium repens	28.6	.	28.6	21.4	50.0	7.1	14.3	.
Trisetum flavescens	7.1	7.1	7.1	7.1	50.0	28.6	28.6	28.6
Veronica chamaedrys	57.1	50.0	35.7	28.6	64.3	64.3	57.1	64.3
Vicia cracca	14.3	7.1	7.1	7.1	71.4	.	14.3	7.1

Table 3. Jaccard similarity coefficients between the aboveground vegetation and, respectively, the seed rain (0–1 cm) and two seed bank layers (1–5 cm and 5–10 cm) of degraded and non-degraded meadows. Different superscript letters at the means denote significant differences between soil layers within each category of meadow according to Wilcoxon signed rank test.

Tabelle 3. Jaccard-Ähnlichkeits-Koeffizienten zwischen der oberirdischen Vegetation und jeweils dem Samenregen (0–1 cm) und zwei Samenbanktiefen (1–5 cm und 5–10 cm) degenerierter und nicht degenerierter Wiesen. Unterschiedliche hochgestellte Buchstaben kennzeichnen für den jeweiligen Wiesentyp statistisch signifikante Unterschiede nach dem Wilcoxon Vorzeichen-Rang Test.

	Degraded meadows			Non-degraded meadows		
Layer [cm]	0–1	1–5	5–10	0–1	1–5	5–10
mean	0.32^{b}	0.33^{b}	0.24^{a}	0.23^{a}	0.24^{a}	0.22^{a}
± SE	0.04	0.04	0.03	0.02	0.02	0.02
minimum	0.08	0.13	0.00	0.09	0.13	0.03
maximum	0.60	0.64	0.40	0.34	0.44	0.38

3.3 Similarity between aboveground vegetation and seed rain and seed bank

The similarity between the aboveground vegetation and the seed rain and seed bank was examined using the Jaccard similarity index (Table 3). The Jaccard coefficients calculated for the different soil layers did show differences for the degraded but not for non-degraded meadows.

Two of the three grasses causing meadow degradation after abandonment achieved high seed numbers in the seed bank. *F. rubra*, which had an 80% cover in the vegetation of the degraded meadows, reached 15.7% share in the total seed rain and seed bank. *Calamagrostis epigejos* reached 36.3% in the total seed rain and seed bank whereas it made up 83% of the aboveground vegetation. *Deschampsia cespitosa* had the lowest proportion in the seed rain and seed bank (2.5%) but reached 67% of the aboveground vegetation. Correlations between the covers of dominant species in the aboveground vegetation of degraded meadows and their seed rain and seed bank were significant for *C. epigejos* and *F. rubra*, but not for *D. cespitosa* (Table 4). During the study, no seedling of *L. polyphyllus* was found, even in samples taken from the plots where it was part of the aboveground vegetation. Typical meadow species were also found in the degraded meadows for which Spearman's rank correlation coefficients (Table 4) for species frequency in aboveground vegetation and seed bank were highly significant.

4. Discussion

4.1 Aboveground vegetation

Degradation of abandoned mountain grasslands is usually related to changes in the original proportions of species, which leads to the dominance of a few species and an overall decrease in species diversity (Stránská 2004, Pruchniewicz & Żołnierz 2014). Grasses, including *Calamagrostis epigejos*, *Festuca rubra* and, less frequently, *Deschampsia cespitosa*, are the most expansive species dominating swards of abandoned mesic mountain grasslands in the middle part of the Sudetes Mts. (Pruchniewicz & Żołnierz 2014). These grasses are fast-growing, produce large amounts of biomass and are able to outcompete other

Table 4. Spearman's rank correlation between the frequency (%) of typical meadow species and expanding species (marked with #) in the aboveground vegetation and, respectively, the seed rain (0–1 cm) and two seed bank layers (1–5 cm, 5–10 cm) of degraded and non-degraded grasslands. Significant correlation coefficients are denoted as * = $p \leq 0.05$, ** = $p \leq 0.01$ and *** = $p \leq 0.001$.

Tabelle 4. Spearman Rangkorrelation der Frequenz (%) typischer Wiesenarten und expansiver Arten (mit # gekennzeichnet) zwischen der oberirdischen Vegetation und jeweils dem Samenregen (0–1 cm) und zwei Samenbanktiefen (1–5 cm und 5–10 cm) degenerierter und nicht degenerierter Wiesen. Signifikante Korrelationskoeffizienten sind mit * = $p \leq 0,05$; ** = $p \leq 0,01$ und *** = $p \leq 0,001$ gekennzeichnet.

	Degraded meadows			Non-degraded meadows		
Layer [cm]	0–1	1–5	5–10	0–1	1–5	5–10
Agrostis capillaris				0.717**	0.746**	0.747**
Anthoxanthum odoratum	0.699**	0.6999**		0.566*		0.645*
Arrhenatherum elatius	0.911***	0.959***		0.885***	0.833***	0.892***
Calamagrostis epigejos #	0.958***	0.898***	0.898***			
Campanula patula	0.734**					
Cardaminopsis halleri					0.621**	
Centaurea jacea	0.734**	0.734**	0.734**			
Cynosurus cristatus				0.734**		0.734**
Dactylis glomerata		0.891***	0.564*	0.58*	0.631**	
Festuca pratensis	0.679**	0.997***	0.679**			
Festuca rubra #	0.855***	0.859***	0.591*	0.72*	0.694**	0.783***
Poa pratensis	0.624*					
Stellaria graminea		0.606*				
Tragopogon pratensis	0.576*					
Trisetum flavescens				0.843***	0.716**	
Vicia cracca			0.734**			

species, particularly small and light-demanding forbs. These expansive species may cause a decline of diversity and suppress species characteristic for *Arrhenatheretalia* type grasslands.

4.2 Seed rain and seed bank

Seedling density and species richness of the seed rain and the seed bank vary strongly according to community type and type of management (Willems & Bik 1998, Reiné et al. 2004, Bossuyt et al. 2006, Wellstein et al. 2007). In our study we found almost the same average seedling densities in non-degraded managed meadows and degraded grasslands. This indicates that both the degradation of the vegetation as well as the type of management had no significant effect on seed rain and soil seed bank. In contrast to our results, Bossuyt & Hermy (2003) observed a decrease in seed density in the seed bank after cessation of grassland management.

In our study we also found nearly the same species richness in seed rain and soil seed bank of degraded and non-degraded grassland. Our results are similar to those obtained by Tóth & Hüse (2013), who found a comparable species-richness in the vegetation and the soil seed banks of degraded and non-degraded loess grasslands in Hungary. However, while in our survey the species richness of degraded vegetation was significantly lower compared with that of non-degraded grassland, the total number of seeds in both categories of grasslands was almost equal.

4.3 Relationships between species richness in aboveground vegetation, seed rain and seed bank

In our experiment, the similarity in species composition between aboveground vegetation, seed rain and seed bank in the soil was low, and it was nearly the same in non-degraded and degraded meadows (Jaccard index ranges: 0.22–0.24 and 0.24–0.33, respectively). These results are in line with TÓTH & HÜSE (2013), who found Jaccard similarities of 0.31 and 0.35 in degraded and non-degraded loess grasslands, respectively. A low degree of similarity between the aboveground vegetation of degraded patches and their seed bank in our meadows suggests that there is still the possibility to reverse their degradation after a removal of expansive species from the vegetation.

Reports by various authors concerning the relationship between species richness in aboveground vegetation and seed bank of degraded and non-degraded meadows remain equivocal. JACQUEMYN et al. (2011) observed a rapid decline of species richness in aboveground vegetation and seed bank after abandonment, whereas WELLSTEIN et al. (2007) did not observe an effect of grassland management on species richness of the seed bank. HANDLOVÁ & MÜNZBERGEROVÁ (2006) noticed that species absent from the vegetation of degraded meadows were also absent from the seed bank of both degraded and non-degraded grasslands. In our survey, mean species richness in the aboveground vegetation of degraded meadows was lower than in non-degraded plots. In contrast, in the upper soil layers, species richness was only slightly lower in degraded than in non-degraded meadows. This indicates a delayed response of the seed bank to the on-going degradation of the aboveground vegetation.

4.4 The seed bank and prospects of grassland restoration

The usefulness of the soil seed bank in the restoration of degraded grasslands is a matter of discussion that encompasses different views. Some authors believe that the role of the seed bank is important (RUPRECHT et al. 2010, KALAMEES et al. 2012, METSOJA et al. 2014), while others see it as limited (e.g. HÖLZEL & OTTE 2009, JACQUEMYN et al. 2011, TÓTH & HÜSE 2013, KARLÍK & POSCHLOD 2014) or even negligible (KALAMEES & ZOBEL 1998). Owing to the generally short longevity of seeds of grassland species (BOSSUYT & HERMY 2003, JACQUEMYN et al. 2011, PAKEMAN & EASTWOOD 2013) the seed bank is considered to contribute to meadow restoration only in the case of recently abandoned sites (WAGNER et al. 2003). An important issue is related to the occurrence of naturally relatively rare or less abundant meadow species in the seed bank. Usually, only a very low number of seeds of such species can be found in the seed bank of grasslands (HANDLOVÁ & MÜNZBERGEROVÁ 2006, WELLSTEIN et al. 2007, BOSSUYT & HONNAY 2008). Our study confirms this, as we obtained very low numbers of seedlings of rare species in the soil samples taken both from non-degraded and degraded meadows. The majority of emerged seedlings were those of the most frequent and abundant species in the aboveground vegetation. Seeds of typical meadow species were still present in deeper layers of the soil in proportions similar to those observed in non-degraded meadows. This can be seen as an advantageous circumstance regarding the restoration of grasslands in the Sudetes Mts.

Many authors recommend the introduction of additional seed pools sampled from grasslands of high diversity in order to compensate the lack or insufficient amounts of target species in the seed bank (SMITH et al. 2002, BOSSUYT et al. 2006, HANDLOVÁ & MÜNZBERGEROVÁ 2006, DONATH et al. 2007, KIEHL et al. 2010, VALKÓ et al. 2011, SCHMIEDE et al. 2012). Such a solution also seems to be a proper measure in the case of degraded meadows in our study area, where target species (however, without the rare and endangered ones) still occur in the soil seed bank, but in rather low abundances.

5. Conclusion

The pronounced degradation of meadow vegetation in the Central Sudetes is still only relatively weakly reflected in the quantitative and qualitative properties of the seed bank. The seed bank of the studied degraded meadows shows some kind of inertia. While strongly competitive, expanding species already dominate the aboveground vegetation and start to build up their seedbanks, viable seeds of typical meadow species are still present in the soil seed bank. This reveals potential opportunities for at least some contribution of the soil seed bank to the restoration of these meadows after an elimination of expansive species from the aboveground vegetation. However, the low abundances of typical meadow species in the seed bank may call for the use of active restoration measures, such as seeding with local seeds or the application of seed-containing material from species-rich, non-degraded sites.

Erweiterte deutsche Zusammenfassung

Einleitung - Die Degradierung vormals artenreichen Grünlands und die damit verbundenen Verluste an Artenvielfalt sind ein in Europa weit verbreitetes Phänomen. Während in weiten Bereichen eine Nutzungsintensivierung zu einem Verlust von Biodiversität führt, ist in Bergregionen vor allem eine Nutzungsaufgabe mit nachfolgendem Verlust von Pflanzenarten zu verzeichnen.

Die Nutzungsaufgabe von Bergwiesen ist oft mit einer Verschiebung der Abundanzen von Arten verbunden, in deren Verlauf einzelne Arten dominant und zahlreiche andere Arten verdrängt werden. Für die Entwicklung geeigneter Maßnahmen zum Schutz dieser Lebensräume ist ein Verständnis der Degenerationsprozesse und des Regenerationspotentials von Bergwiesen nötig. Dabei könnte die Bodensamenbank eine wichtige Rolle für die Regeneration der Artenzusammensetzung dieser Lebensräume spielen. Daher beschäftigt sich der vorliegende Beitrag mit den Auswirkungen der Dominanz expansiver Pflanzenarten auf die Eigenschaften der Samenbank. Folgende Fragen werden untersucht: (1) Spiegeln sich Unterschiede im Artenreichtum der oberirdischen Vegetation degenerierter und nicht-degenerierter Wiesen in den Sudeten in deren Samenregen und deren Samenbank wider? (2) Wie groß ist die Ähnlichkeit der Artenzusammensetzung zwischen oberirdischer Vegetation, Samenregen und Samenbank in beiden Wiesenkategorien? (3) Enthält der Samenregen und die Samenbank degenerierter Wiesen noch typische Graslandarten, die eine Wiederherstellung der Bergwiesen unterstützen könnten?

Methoden - Die Untersuchungen wurden im polnischen Teil der zentralen Sudeten in mesophilem Berggrünland (410–860 m NN) durchgeführt. Es wurden jeweils 14 Aufnahmeflächen (5 m x 5 m) in degenerierten und nicht-degenerierten Bergwiesen ausgewählt. Nicht-degenerierte Grünlandbestände wurde regelmäßig nicht-intensiv genutzt und nicht gedüngt, während degenerierte Bestände durch Nutzungsaufgabe oder unregelmäßige Nutzung gekennzeichnet waren. Letztere zeichneten sich durch Dominanz von Arten wie *Calamagrostis epigejos*, *Festuca rubra*, *Deschampsia cespitosa* oder *Lupinus polyphyllus* aus. Auf jeder Fläche wurden Vegetationsaufnahmen durchgeführt und jeweils eine Mischprobe für Samenbankanalysen (7 Einstiche pro Aufnahmefläche) gezogen. Die Samenbankproben wurden unterteilt in die Schicht 0–1 cm, welche den Samenregen repräsentiert, sowie 1–5 cm und 5–10 cm, die beide die Samenbank im engeren Sinne repräsentieren. Die Samenbankanalyse erfolgte mit Hilfe der Auflaufmethode.

Artenreichtum und Diversität wurde zwischen degenerierten und nicht-degenerierten Bergwiesen und zwischen oberirdischer Vegetation und Samenbank mit Hilfe von t-Tests und Mann-Whitney U-Tests verglichen. Der nicht-parametrische Wilcoxon-Vorzeichen-Rang Test wurde herangezogen, um die Unterschiede in den erfassten Parametern zwischen der Samenbank der verschiedenen Bodenschichten zu analysieren. Für die dominanten Arten wurden die Pearson oder die Spearman Korrelationskoeffizienten zwischen deren Abundanz in der oberirdischen Vegetation und deren Anteil am Samenregen bzw. in der Samenbank berechnet. Eine Analyse der Artenzusammensetzung von oberirdischer Vegetation und Samenbank in degenerierten und nicht-degenerierten Bergwiesen erfolgte mit Hilfe einer NMDS-Ordination.

Ergebnisse und Diskussion - In der NMDS-Ordination zeigte sich eine deutliche Differenzierung der Artenzusammensetzung der Vegetationsdecke, des Samenregens und der Samenbank von degenerierten und nicht-degenerierten Bergwiesen (Abb. 1, 3). Degenerierte Bergwiesen waren durch geringeren Artenreichtum und geringere Diversität in der oberirdischen Vegetation, dem Samenregen und der Samenbank gekennzeichnet (Abb. 2). Die höchsten Samendichten konnten bei beiden Wiesentypen im Samenregen nachgewiesen werden (Tab. 1). Es zeigte sich auch, dass die Unterschiede in der Samendichte zwischen degenerierten und nicht-degenerierten Grünland nicht signifikant waren (Tab. 1). Interessanterweise umfassten die Samenbanken degenerierter Bergwiesen immer noch typische Arten des mesophilen Grünlands in ähnlichen Anteilen wie nicht degenerierte Wiesen (Tab. 2, 4). Trotz eingetretener Verschiebungen im Artenbestand zeigten die Ähnlichkeitsindizes zwischen oberirdischer Vegetation, Samenregen und Samenbank keine signifikanten Unterschiede zwischen den Wiesentypen (Tab. 3).Wir schließen aus diesen Ergebnissen, dass die Samenbank der Bergwiesen in den Sudeten nach einer erfolgreichen Reduktion der dominanten Arten immer noch für eine Wiederherstellung dieser Lebensräume genutzt werden kann.

Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Abbreviations of species names in Figure 1 and 3.

Anhang E1. Abkürzungen der in Abbildung 1 und 3 aufgeführten Arten.

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