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Soil Seed Banks of Continental Grasslands with Different Water Regimes—A Comparative Study from the Aspect of Recovery Potential

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Abstract: Due to the threats posed by climate change and landscape alteration, there is an increasing need to better understand using seed banks of continental grasslands as a possible aid to conservation and restoration. Here, the soil seed bank of a wet grassland type, an ecotone and a semi-dry grassland type, all formed along a slope in NE Hungary, were compared from the aspect of recovery potential. For this, a vegetation survey and a seedling emergence examination were performed. The seed banks of the three grassland types differed significantly in terms of density. It was significantly higher in both the wet and the ecotone grassland types than in the semi-dry one. The seed banks of the three grassland types proved to be very similar in terms of diversity. The floristic similarity between the vegetation and the seed banks was much higher in both the wet and the ecotone grassland types than in the semi-dry one. Most of the abundant species of the vegetation had transient seed banks, but more of the characteristic species of the wet and the ecotone grassland types maintained dense and/or persistent seed banks than those of the semi-dry one. In the case of degradation, a complete recovery is not ensured by the seed bank of either studied grassland type; however, compared to that of the semi-dry grassland, the wet grassland's seed bank better supports an increase in diversity within a limited period. In the case of restoration, within five years after destruction, it could be more rewarding to deal with wet grassland types prior to dry ones.

Keywords: meadow; wetland; *Carex*; persistence; resilience; climate change; restoration

1. Introduction

It is known that the seed banks of different habitats can vary greatly from each other [1,2], mainly as a result of different seed bank formation abilities of the species, and due to environmental filters [3,4]. Thus, recovery values that are represented by their seed banks are not the same. Although research suggests that for most habitat types, the seed bank expectedly does not contain the full recovery base [1,2,5], it can be a promising tool for increasing the diversity, and in some cases, as even a means for protecting rare endangered species [6–10]. The local seed bank is especially valued in cases where horizontal seed dispersion is limited [9,11].

Studying soil seed banks of European grassland [12,13] and wetland [14,15] habitat types is fundamental task of conservation biology and restoration ecology [5]. This is because these habitat types are threatened by serious fragmentation, spatial reduction and diversity losses due to landscape alterations and climate change [12–15]. There is a particular urgency to explore the seed banks of wetlands more accurately, including those of the types with grassland physiognomy, as these have barely been explored thus far in Hungary, and even in Europe (cf. list of research on Hungarian [2] and European [3] habitats). Catching up these wet grasslands has been urgently advocated by several authors [9,14,16]. This is especially relevant in the continental region, hence in Hungary as well, where water supply is a crucial ecological constraint, and where the impact of climate change on wet grasslands may soon become significant.

Despite the imminent need for restoration interventions, there is a lack of comparative studies on the seed banks of these endangered wet and dry grasslands. Motivated by the above, we aimed to study the soil seed banks of continental grasslands under different water regimes. In a narrower sense, our goal was to determine whether there are any significant differences between the seed banks of grassland types with different water regimes in terms of quantitative and qualitative properties and thus, in terms of their abilities to recover. On the basis of observations that show that in moderately drier soils, species which are adapting to unfavorable germination and establishment conditions with larger seed sizes may be common [17–19], and that large seed size predestines a sporadic and/or transient seed bank [20–23], we hypothesized that drier grassland types are less capable of longer-term recovery from their seed banks than wetter ones.

2. Materials and Methods

2.1. Sample Area and Sampling Design

The sample area is located in the Tardona Hills, NE Hungary, under a moderately cool and dry climate [24]. More specifically, a 60 m × 10 m large sample area was designated on the toe of a SSW-facing slope (WGS84: N 48.183450°, E 20.703799°; altitude: 197.2 m). It has an average inclination of 17%, and at the bottom, it adjoins an intermittent pond with an irregular water supply. It is currently covered by a vegetation complex of grasslands, in which the moisture indicator components gradually lost their cover as the habitat became drier upslope. For decades, conservatory mowing has been conducted here [25].

In this sample area, 3 of 60-m long parallel, non-contiguous transects were designated in the longitudinal direction of the slope, i.e., along the soil moisture gradient. In each transect, 10 of 2 m × 2 m large, permanent and non-contiguous sampling quadrats were designated. The transects and the quadrats in them were placed relatively close to each other (2–5 m), the reason being space limitation.

Such a design of sampling on a slope was used because we had been searching for grasslands that share similar climatic conditions, landscape history and environment, but differing in their water regimes, which would therefore, be the most suitable for habitat-scale comparisons after delineation.

2.2. Data Collection

Surveys and sampling were performed by quadrats for above-ground vegetation (spring and autumn 2013), for soil seed bank (spring 2013), as well as for soil (soil moisture content: autumn 2012 and 2013; other soil properties: autumn 2012).

In the frame of the vegetation surveys, occurring species were recorded, and the cover percentage was estimated. The spring and autumn recordings were summarized using the higher of the 2 cover values of a given species, estimated at 2 different dates. Together with the data that were derived from these, we had the following vegetation data for each quadrat: species list, species-specific and total green plant cover (%), total litter cover (%), total uncovered surface (%), species number and Shannon diversity (using natural logarithm in the equation).

In the context of the seed bank examinations, first, samples that were representative for the 0–10 cm soil depth interval were subdivided into 0–5 and 5–10 cm intervals (together, a 577.2 cm^3 sample per quadrat, resulting from the pooling of 6 soil cores). Then, from these subdivided samples, after the seed concentrating procedure according to ter Heerdt et al. [26], 8 months of greenhouse germination on sterile peat was performed, as recommended by Thompson et al. [3] and Csontos [21,27]. The procedure included 4 types of dormancy-breaking treatments (natural and artificial cold stratification prior to seed concentration, scarification and soaking included in seed concentration, end-of-summer drought treatment with 3 weeks watering break). The germinated species were registered, and their specimen numbers were counted. Together with the data that were derived from these, we had the following seed bank data for the 0–5, 5–10 and 0–10 cm soil depth intervals in each quadrat: species list, species-specific and total seed bank density (seeds/m^2), species number and Shannon diversity.

In the context of the soil examinations, from samples that were representative for the 0–10 cm soil depth interval, the following soil properties were determined using the standard Hungarian laboratory tests: soil moisture content (m/m%, referring to moist soil), consistency according to Arany, organic matter content (m/m%), carbonate content (m/m%), water-soluble salt content (m/m%) and pH determined in KCl [28–30].

In addition to these local data, the relative soil moisture requirement (WB) according to the system of Borhidi [31] was gathered for each species from the FLORA database [32], valid in the Pannonian biogeographic region. The WB is a 12-category system, in which the categories are relative values (1–12, where the moisture quantity that characterizes the habitat increases from "1" to "12"), and are applicable for habitat indication (Appendix A, Table A1).

Scientific names of taxa followed the nomenclature of the Euro+Med [33].

2.3. Data Analysis

Statistical analyses were performed with PAST 3.01. [34] and R 3.4.3. [35] software.

For habitat-scale comparisons, first, we had to delineate the types of grasslands that differed in their water regimes along the transects of the slope. Based on visual interpretation, we hypothesized there would be zonal separation of 3 grassland types along the transects: wet grassland (WG) (6 quadrats), ecotone (EG) (18 quadrats) and semi-dry grassland (DG) (6 quadrats). We note here that there were technical reasons for referring to the EG as a type of grassland in this study, although it is an ecotone between a wet and a dry grassland that is atypical in the classical sense of an ecotone. The statistical separation of the 3 grassland types by water regime, and the goodness of the delineation were initially checked using fuzzy c-means clustering ("fanny" function in the "cluster" R package [36]), which was performed on the cover-weighted mean WB of the vegetation-forming species, and secondly, by linear discriminant analysis ("lda" function in the "MASS" R package [37]) that was performed on soil plus vegetation properties. Thus, the total soil sample volume for the seed bank was 3463.2 cm^3 for the WG and DG with 6 quadrats, which fit the sample volume that was typical for similar European habitat types (cf. circa 3800 cm^3 for dry-mesophilous meadows [9,38], 3000 cm^3 for wet meadows [39]). The total seed bank of the EG, based on 18 quadrats, was represented by a 3-times-larger sample volume.

In order to identify the habitat type of the grasslands, we used the General National Habitat Classification System's (ÁNÉR) version from 2011 [40]; however, we also provided their equivalents, according to the European Nature Information System's (EUNIS) habitat classification [41].

The vegetation and then the seed banks of the 3 grassland types were compared in terms of quantitative properties, including vegetation cover, seed bank density, species number and Shannon diversity. In order to check whether the differences between the 3 grassland types were significant for any of the quantitative properties, one-way ANOVA and the post hoc Tukey–Kramer pairwise test were used. In case the criteria of the parametric procedure were not met, and their fulfilment could not be achieved even by data transformation, the Kruskal–Wallis test and post hoc Mann–Whitney pairwise test were performed [42]. Among the applicability criteria of the significance tests, normality was checked via the Shapiro–Wilk test, and homoscedasticity was checked using Levene's test [42]. All *p*-values were rounded to 4 decimal places.

The vegetation and then the seed banks of the 3 grassland types were also compared in terms of qualitative properties, including WB spectrum, seed bank persistence and abundant species. When describing grassland types, WB categories that were similar to each other were merged by creating the following WB groups, i.e., intervals: "Group WB10–7" for species that were most associated with high soil moisture content, "Group WB6–4" for species that were associated with moderate, and "Group WB3–1" for species that were most associated with low soil moisture content. The "Group WB12–11" interval for water plant species was not relevant, due to the absence of species. The 3-category seed bank classification system, according to Thompson [43], was used to express the seed bank persistence of a species achieved within a given grassland type. For identifying the seed bank type of a species within a given grassland type, the pooled data of the larger sampling unit (given grassland type) were decisive over the individual data of the smaller ones (quadrats) within it. The seed bank type was identified for only those species for which sufficient data were available in the given grassland type for reliable classification, i.e., based on the vegetation and/or the seed bank, the frequency of the species $\geq$3 in the grassland type; in the case of exclusive occurrence in the vegetation, the total cover of the species $\geq$1% in the grassland type; in the case of occurrence in the seed bank, the total seed number (here, meaning the total number of seedlings found, and not the derived seed bank density) of the species $\geq$3 in the grassland type. For classifying the species that are prone to anemochory according to the database of Csontos et al. [44], we always considered the possibility of seeds arriving from outside the sampling unit.

In order to express the floristic similarity between the vegetation and the seed bank, the Jaccard index was calculated from the species lists on the basis of grassland types.

3. Results

3.1. Checking the Separation of Grassland Types by Water Regime

The fuzzy c-means clustering that was performed on the WB of the vegetation confirmed that there was a reason for the separate treatment of the three grassland types under different water regimes. The membership weight of the quadrats in the three optional clusters are found in Figure 1a.

Since spatial heterogeneity and mosaicism was acceptable as a habitat feature in the transition-featured EG, the results of the clustering met the visual interpretation-based expectation that the two lowermost quadrats of each transect were considered to be representative for WG, the six middle quadrats of each transect were considered to be representative for EG, and the two uppermost quadrats of each transect were considered to be representative for DG (Figure 1a,b).

The 6, 18, 6 quadrats according to the above expectation were also considered to be related on the basis of linear discriminant analysis that was conducted on the soil plus vegetation properties (Appendix A, Table A2). In LD1, which explained 58.5% of the separation of these three quadrat groups from each other, the dominance of the coefficient that was related to the soil moisture content confirmed that the soil moisture played a determining role in the grouping of the quadrats. Supporting data on soil properties by the three grassland types can be read in Appendix A, Table A3.

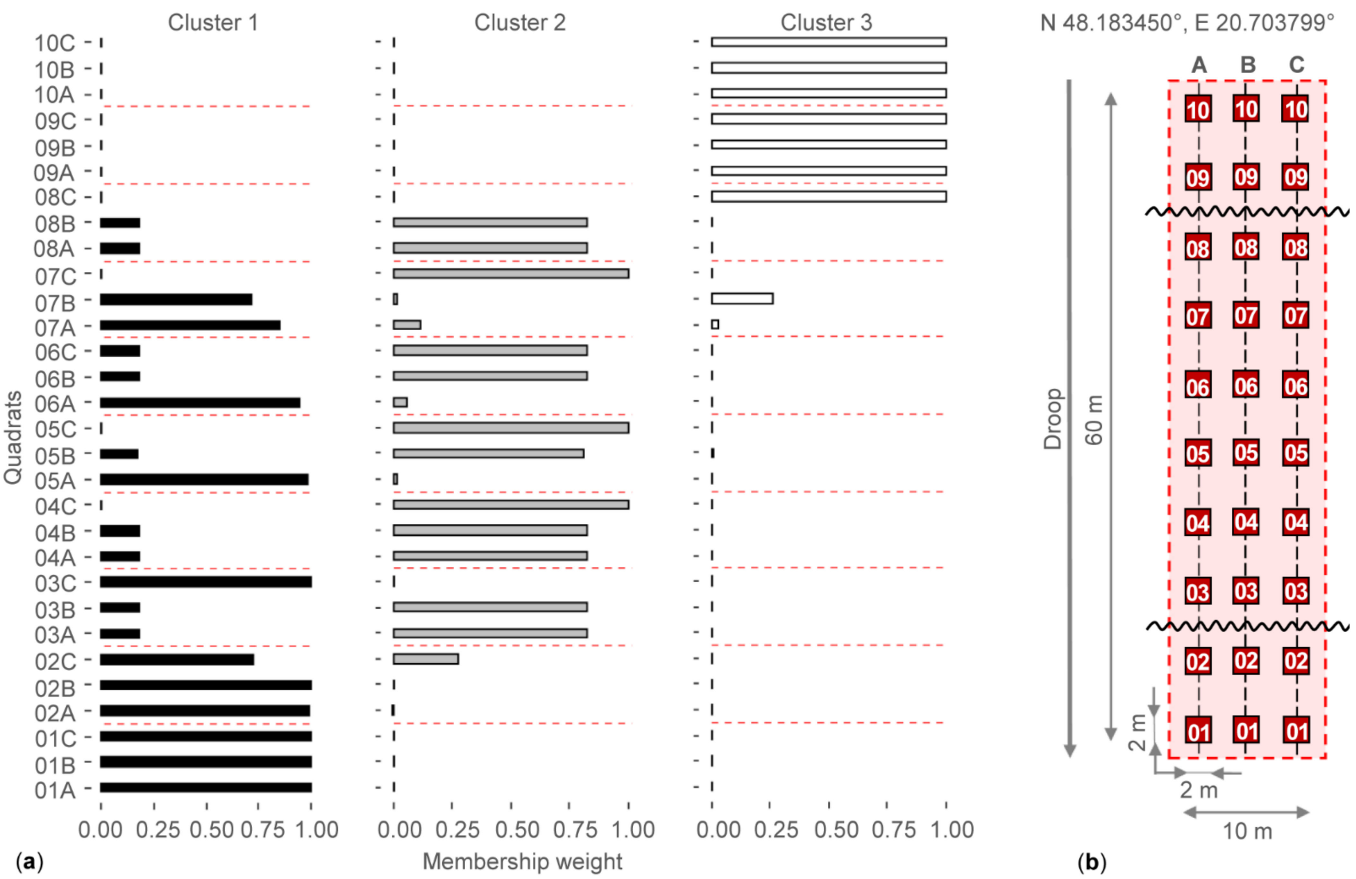

Figure 1. Membership weight of the quadrats in the three optional clusters, based on moisture requirement (fuzzy c-means clustering) (**a**), and the real slope position of the quadrats (**b**). In each quadrat, the moisture requirement (WB) is expressed as the cover-weighted mean WB of the vegetation-forming species, where the WB is defined according to the system of Borhidi [31]. Notation: A, B, C—codes of the transects designated along the slope; 01–10—codes of the quadrats designated in the transects.

3.2. Features of the Above-Ground Vegetation in the Grassland Types

According to the ÁNÉR, the examined WG could be classified in the category "B5—Non-tussock tall-sedge beds", and according to the EUNIS, it belonged in the category "D5.21—Beds of large *Carex* species". One species in it had a mean cover that was higher than the 10.0% regarded as high, specifically the monodominant *Carex acutiformis* (50.1%). Here, the species belonging to groups WB10–7 and WB6–4 contributed to the total species number, with similarly high percentages (50.0% and 40.9%, respectively) (Figure 2a). However, those belonging to WB10–7 yielded a much higher percentage of the total cover (84.8%) (Figure 2b).

According to the ÁNÉR, the examined DG could be classified in the category "H4—Semi-dry grasslands", and according to the EUNIS, it belonged in the category "E1.23—Meso-xerophile subcontinental meadow-steppes". Four species in it had a mean cover that was higher than 10.0%, specifically *Brachypodium pinnatum* (22.8%), *Elytrigia repens* (15.0%), *Peucedanum cervaria* (13.3%) and *Filipendula vulgaris* (10.2%). Here, the species that belonged to groups WB6–4 and WB3–1 contributed to the total species number, with similarly high percentages (47.2% and 43.6%, respectively) (Figure 2a). The contribution to the total cover by those belonging to WB3–1 was high (31.9%), but not as high as by those that belonged to WB6–4 (59.7%) (Figure 2b).

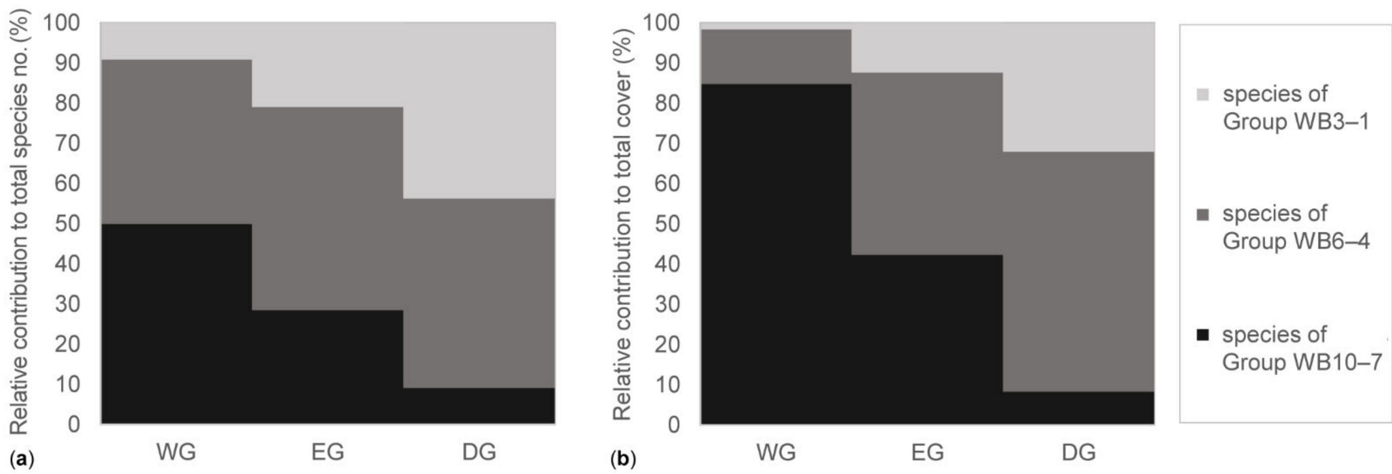

Figure 2. Relative contributions to the total species number (**a**) and to the total cover (**b**) by the species belonging to the given WB groups in the above-ground vegetation of the three grassland types. Notation: WG—wet grassland type; EG—ecotone grassland type; DG—semi-dry grassland type. WB groups were created by grouping the WB categories from the system of Borhidi [31], where "Group WB10–7" was for species that are most associated with high, "Group WB6–4" was for species that are associated with moderate, and "Group WB3–1" was for species that are most associated with low soil moisture content.

In the unit called EG, one species had a mean cover that was higher than 10.0%, specifically *Carex muricata ssp. pairae* (14.6%), which can be considered ecotone-specific here. In terms of moisture requirement, the EG was closer to WG than to DG. Although the highest percentage of the total species number was given by the species belonging to group WB6–4 (50.6%) (Figure 2a), the contribution to the total cover by those species belonging to WB10–7 was similarly high (42.3%) (Figure 2b).

The three grassland types differed significantly from each other in terms of mean cover (Kruskal–Wallis test, $H = 14.1$, $df = 2$, $p = 0.0008$), within which the mean cover of the WG was significantly lower than that of DG (Mann–Whitney pairwise test, $p = 0.0046$), while that of EG was significantly higher than that of WG (Mann–Whitney pairwise test, $p = 0.0122$), and significantly lower than that of DG (Mann–Whitney pairwise test, $p = 0.0065$) (Table 1). The cover of the litter was nearly three times higher in the WG ($\overline{X} \pm SD$, 12.0 ± 4.7%) than in EG (4.8 ± 2.3%) and in DG (4.8 ± 2.6%). The uncovered surface was small in the DG ($\overline{X} \pm SD$, 1.8 ± 0.8%), while it was nearly four times larger in WG (6.7 ± 2.4%) and in EG (7.3 ± 4.7%).

Table 1. Quantitative properties of the above-ground vegetation in the three grassland types under different water regimes.

	Cover (%)	Species Number		Shannon Diversity
	$\overline{X} \pm SD$	Σ	$\overline{X} \pm SD$	$\overline{X} \pm SD$
Wet grassland type, $N = 6$	89.2 ± 4.9 [a]	44.0	21.7 ± 5.3 [a]	1.7 ± 0.7
Ecotone grassland type, $N = 18$	104.7 ± 14.1 [b]	91.0	27.9 ± 3.4 [a]	2.4 ± 0.3
Semi-dry grassland type, $N = 6$	126.7 ± 11.7 [c]	55.0	27.5 ± 5.8 [a]	2.2 ± 0.3

Notation: Within a given column, the mean values are labelled with letters in superscript, according to their significant differences (Kruskal–Wallis test and post hoc Mann–Whitney pairwise test, $p < 0.05$); the mean values without superscripts were not tested for significant differences.

The three grassland types did not differ significantly from each other in terms of mean species number (Kruskal–Wallis test, $H = 5.2$, $df = 2$, $p = 0.0722$), although the mean diversity was slightly lower in the WG than in DG and in EG (Table 1).

3.3. Features of the Soil Seed Bank in the Grassland Types

It was true for all three grassland types that the largest proportion of the seed bank was provided by hygrophytes and/or ruderals.

In the WG, five species had a mean density that was higher than the 500.0 seeds/m^2 regarded as high, specifically *Lythrum salicaria* (9879.1 seeds/m^2), *Erigeron annuus* (2166.5 seeds/m^2), *Veronica longifolia* (1704.3 seeds/m^2), *Carex acutiformis* (693.3 seeds/m^2) and *Anagallis arvensis* (635.5 seeds/m^2). Here, the species that belonged to groups WB10–7 and WB6–4 contributed to the total species number, with similarly high percentages (44.7% and 44.8%, respectively) (Figure 3a). However, those belonging to WB10–7 yielded a much higher percentage of the total density (91.4%) (Figure 3b).

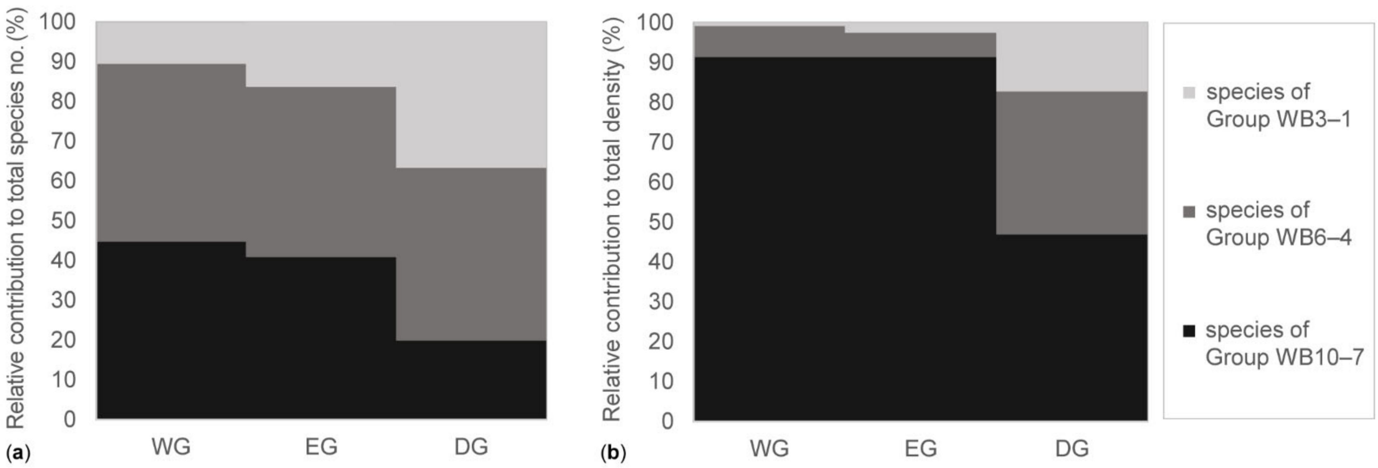

Figure 3. Relative contribution to the total species number (**a**) and to the total density (**b**) by the species belonging to the given WB groups in the soil seed bank of the three grassland types. Notation: WG—wet grassland type; EG—ecotone grassland type; DG—semi-dry grassland type; WB groups were created by grouping the WB categories from the system of Borhidi [31], where "Group WB10–7" was for species that are most associated with high, "Group WB6–4" was for species that are associated with moderate, and "Group WB3–1" was for species that are most associated with low soil moisture content.

In the DG, one species had a mean density that was higher than 500.0 seeds/m^2, specifically *Erigeron annuus* (1068.8 seeds/m^2). Although the highest percentages of the total species number were yielded by species belonging to groups WB6–4 and WB3–1 (43.4% and 36.6%, respectively) (Figure 3a), the contribution to the total density by those belonging to WB10–7 was much higher (46.9%) (Figure 3b).

In the EG, three species had a mean density that was higher than 500.0 seeds/m^2, specifically *Erigeron annuus* (9397.7 seeds/m^2), *Lythrum salicaria* (1694.7 seeds/m^2) and *Silene flos-cuculi* (606.6 seeds/m^2). In terms of WB, the EG was very similar to WG; see Figure 3a,b.

The three grassland types differed significantly from each other in terms of mean density (one-way ANOVA, ln transformation, $F = 16.6$, $ndf = 2$, $ddf = 27$, $p = 0.0000$), within which the mean density of the WG was significantly higher than that of DG (Tukey–Kramer pairwise test, $p = 0.0001$), while that of the EG was significantly higher than that of DG (Tukey–Kramer pairwise test, $p = 0.0002$) and lower than that of WG, but not significantly (Tukey–Kramer pairwise test, $p = 0.9154$) (Table 2).

The three grassland types did not differ significantly from each other in terms of mean species numbers (one-way ANOVA, $F = 0.8$, $ndf = 2$, $ddf = 27$, $p = 0.4719$). The mean diversity was low in all three grassland types (Table 2).

The seed bank of the 5–10 cm soil depth interval, i.e., the persistent base, was substantially higher in the WG than in DG, but lower than in EG in terms of both density and diversity (Table 2).

Table 2. Quantitative properties of the soil seed banks in the three grassland types under different water regimes.

	Density (Seeds/m^2)	Species Number		Shannon Diversity
	$\bar{X} \pm SD$	Σ	$\bar{X} \pm SD$	$\bar{X} \pm SD$
Wet grassland type, $N = 6$				
0–10 cm	17,129.6 ± 10,372.7 [a]	29.0	10.7 ± 2.0 [a]	1.5 ± 0.4
0–5 cm	14,240.9 ± 8666.9	26.0	9.5 ± 1.0	1.4 ± 0.3
5–10 cm	2888.6 ± 1959.8	12.0	4.7 ± 1.5	1.2 ± 0.4
Ecotone grassland type, $N = 18$				
0–10 cm	14,423.9 ± 6659.3 [a]	49.0	10.4 ± 3.8 [a]	1.3 ± 0.6
0–5 cm	10,591.6 ± 5131.1	40.0	8.1 ± 3.5	1.1 ± 0.6
5–10 cm	3832.2 ± 2354.7	31.0	6.1 ± 2.2	1.3 ± 0.4
Semi-dry grassland type, $N = 6$				
0–10 cm	3697.4 ± 4130.2 [b]	30.0	8.3 ± 5.0 [a]	1.7 ± 0.4
0–5 cm	3004.2 ± 3644.9	25.0	7.0 ± 4.5	1.5 ± 0.5
5–10 cm	693.3 ± 701.9	12.0	2.5 ± 2.9	0.6 ± 0.8

Notation: Within a given column, the mean values are labelled with letters in superscript, according to their significant differences (one-way ANOVA and post hoc Tukey–Kramer pairwise test, $p < 0.05$); the mean values without superscripts were not tested for significant differences.

It was possible to identify the seed bank type of 23 species in the WG, 28 species in the DG and 50 species in EG; these can be read in Appendix A, Table A4. Calculating from these, 30.4% of the species in the WG, 17.9% of the species in DG and 38.0% of the species in EG had persistent seed banks (it was 31.8% in the WG, 20.8% in the DG and 43.2% in the EG when we excluded hard-seeded species that could easily be misclassified as transient). In the WG, 85.7% of the species with persistent seed banks belonged to group WB10–7, and 14.3% to WB6–4. In the DG, 40.0% of the species with persistent seed banks belonged to group WB10–7, and 60.0% to WB6–4. In the EG, 42.1% of the species with persistent seed banks belonged to group WB10–7, 47.4% to WB6–4 and 10.5% to WB3–1. It is worth mentioning that certain species were characterized by different seed bank types under different environmental conditions (*Achillea collina*, *Carex acutiformis*, *Poa pratensis*).

3.4. Similarities between the Above-Ground Vegetation and the Soil Seed Banks from the Aspect of Recovery Potential in the Grassland Types

Based on all three grassland types, it can be concluded that the diversity of the vegetation was higher than that of the seed banks; however, the difference between their diversity was lower in the WG than in the other two grassland types. In the WG, the vegetation and the seed bank together comprised 60 species, 13 of which were shared in the vegetation and in the in situ seed bank; moreover, 16 species appeared exclusively in the seed bank as a hidden diversity. In the DG, the vegetation and the seed bank comprised 77 species, 8 of which were shared in the vegetation and in the in situ seed bank, and 22 were present only in the seed bank. In the EG, the vegetation and the seed bank together comprised 107 species, 33 of which were shared in the vegetation and in the in situ seed bank; moreover, 16 species appeared only in the seed bank. According to the Jaccard index, the floristic similarity between the vegetation and the seed banks was higher in the WG (0.22) than in DG (0.10), but lower than in EG (0.31).

The shared species were largely provided by the hygrophyte matrix species of the vegetation in WG, the characteristic but less frequent species of the vegetation in DG, and the ruderal matrix species of the vegetation in EG; however, not all of them had substantial seed densities.

It was true for all three grassland types that many of the abundant species of the vegetation were not detectable in the in situ seed bank (Table 3a). However, more of the abundant species of the WG's and the EG's vegetation sustained dense and/or persistent seed banks than those of the DG's vegetation. *Carex acutiformis* stood out of these with its dense seed bank, which was also capable of short-term persistence under favorable soil conditions.

Table 3. Quantitative and qualitative properties of the five most abundant species of the above-ground vegetation (**a**) and the soil seed banks (**b**) in the three grassland types with different water regimes.

	Veg. Cover (%)	Seed Bank Density (Seeds/m^2)			ST
		0–10 cm	0–5 cm	5–10 cm	
	$\bar{X} \pm SD$	$\bar{X} \pm SD$	$\bar{X} \pm SD$	$\bar{X} \pm SD$	
(a) The five most abundant species of vegetation by grassland type					
Wet grassland type, *N* = 6					
Carex acutiformis	50.1 ± 18.8	693.3 ± 580.0	693.3 ±580.0	–	T
Colchicum autumnale !	4.9 ± 5.7	–	–	–	T
Cirsium canum !	4.7 ± 5.2	–	–	–	T
Lathyrus palustris	3.3 ± 8.2	–	–	–	?
Lysimachia vulgaris	3.3 ± 2.3	–	–	–	T
Ecotone grassland type, *N* = 18					
Carex muricata ssp. pairae	14.6 ± 15.6	38.5 ± 74.1	28.9 ± 66.5	9.6 ± 40.9	SP
Carex acutiformis	7.9 ± 13.2	423.7 ± 468.9	240.7 ± 215.5	182.9 ± 322.7	SP
Colchicum autumnale !	7.4 ± 12.8	–	–	–	T
Cirsium canum !	7.4 ± 6.6	9.6 ± 40.9	–	9.6 ± 40.9	?
Dactylis glomerata	5.8 ± 6.8	–	–	–	T
Semi-dry grassland type, *N* = 6					
Brachypodium pinnatum	22.8 ± 11.8	–	–	–	T
Elytrigia repens	15.0 ± 23.0	–	–	–	T
Peucedanum cervaria	13.3 ± 13.1	–	–	–	T
Filipendula vulgaris	10.2 ± 6.0	–	–	–	T
Vicia hirsuta	8.7 ± 8.0	28.9 ± 70.8	28.9 ± 70.8	–	?
(b) The five most abundant species of seed bank by grassland type					
Wet grassland type, *N* = 6					
Lythrum salicaria	0.9 ± 0.5	9879.1 ± 7225.5	8492.6 ± 6180.4	1386.5 ± 1160.1	SP
Erigeron annuus !	0.1 ± 0.3	2166.5 ± 991.1	1733.2 ± 701.9	433.3 ± 305.2	SP
Veronica longifolia	0.4 ± 0.5	1704.3 ± 2850.9	1299.9 ± 2303.9	404.4 ± 586.9	SP
Carex acutiformis	50.1 ± 18.8	693.3 ± 580.0	693.3 ± 580.0	–	T
Anagallis arvensis !	–	635.5 ± 498.3	548.8 ± 519.0	86.7 ± 94.9	LP
Ecotone grassland type, *N* = 18					
Erigeron annuus !	3.7 ± 5.3	9397.7 ± 6266.4	7375.6 ± 5279.2	2022.0 ± 1454.9	SP
Lythrum salicaria	0.1 ± 0.2	1694.7 ± 1985.5	1357.7 ± 1698.4	337.0 ± 400.9	SP
Silene flos-cuculi !	0.04 ± 0.06	606.6 ± 731.1	240.7 ± 320.9	365.9 ± 456.2	LP
Juncus articulatus !	–	442.9 ± 876.2	211.8 ± 354.5	231.1 ± 582.5	LP
Carex acutiformis	7.9 ± 13.2	423.7 ± 468.9	240.7 ± 215.5	182.9 ± 322.7	SP
Semi-dry grassland type, *N* = 6					
Erigeron annuus !	–	1068.8 ± 2118.2	953.2 ± 1919.8	115.5 ± 209.9	SP
Carex muricata ssp. pairae	–	462.2 ± 597.0	433.3 ± 534.2	28.9 ± 70.8	SP
Carex hirta	4.0 ± 9.3	375.5 ± 614.4	173.3 ± 346.6	202.2 ± 318.0	LP
Stellaria media !	–	173.3 ± 268.5	57.8 ± 89.5	115.5 ± 209.9	LP
Lythrum salicaria	–	144.4 ± 277.7	115.5 ± 209.9	28.9 ± 70.8	?

Notation: ST—seed bank type referring to the 3-category system of Thompson [43], where "T" means transient, "SP" means short-term and "LP" means long-term persistent; however, "?" is written in the cell of the category when classification was not possible due to insufficient data (data in the grassland type were sufficient for classification if based on the vegetation and/or the seed bank, the frequency of the species ≥3 in the grassland type; in the case of exclusive occurrence in the vegetation, the total cover of the species ≥1% in the grassland type; in the case of occurrence in the seed bank, the total seed number (total number of seedlings found) of the species ≥3 in the grassland type). Species names labelled with "!" in superscript indicate species that are capable of anemochory, according to Csontos et al. [44]. Nomenclature: The scientific names of the species follow the nomenclature of the Euro+Med [33].

It was true for all three grassland types that most of the abundant species of the seed bank were persistent; and in the in situ vegetation, a small part of them was absent or abundant; a large part of them had small cover (Table 3b). The valuable species included *Silene flos-cuculi* and *Veronica longifolia*; moreover, the latter is protected by Hungarian Law [45]. A high-risk invasive species among them was *Erigeron annuus*.

4. Discussion

4.1. The Above-Ground Vegetation in the Grassland Types

In the case of the examined WG we could discuss a characteristic, near-natural representative of its habitat category; meanwhile, in the case of the examined DG, we could discuss a representative of its habitat category that has slightly become uncharacteristic in matrix grasses (cf. modest proliferation of *Elytrigia repens*). The relatively lower diversity of the WG corresponded to the typical diversity of the habitat type, while the relatively higher diversity of the DG approached the typical diversity of the habitat type from below [40].

Related to the irregularly fluctuant water levels of the intermittent pond at the bottom of the slope, the WG and EG can be considered to be habitats that were affected by recurrent, but with only moderately predictable disturbances; meanwhile, in relation to the conservatory mowing, the DG can be considered to be a stable habitat.

4.2. The Soil Seed Bank in the Grassland Types

Noting, first of all, that the comparability of the results from different research on seed banks of a given species, community or area is limited due to differences between the research in sampling method, landscape history and other circumstances [46,47]; however, they still provide an opportunity to detect some trends.

According to the review of Bossuyt and Honnay [1], which covered a wide range of European habitats, it is a common case that a typical wetland species dominates the seed bank. Our results, that a large part of the abundant species were hygrophytes in the case of all three grassland types, fit this well.

Bossuyt and Honnay [1] typically predicted low persistence and density for seed banks of grasslands, explaining it as adaptation to stability, while they typically predicted high persistence and density for seed banks of marshes, explaining it as adaptation to recurrent disturbances. According to the review of Thompson [48], this can be supplemented by the remark that even among recurrent disturbances, only those that are unpredictable exert selection pressure for the formation of a persistent seed bank in wetlands. These findings are in line with our results for the DG, which we considered to be stable, and for the WG and EG, which we considered to be affected by recurrent but only moderately predictable disturbances:

Focusing on the densities of the two extremes, i.e., the WG's and the DG's, the former was considered to be medium high density, while the latter was considered medium low (Table 2). Their densities approached those of similar European habitat types, and their rankings by magnitude were in line with those from the literature (cf. circa 14,000 seeds/m^2 on average in European marshes, ca. 4000 seeds/m^2 on average in European grasslands [1]; ca. 28,000–71,000 seeds/m^2 in abandoned wet meadows dominated by *Carex acutiformis* [39], ca. 4800–5600 seeds/m^2 in resumed dry-mesophilous meadows dominated by *Brachypodium pinnatum* [9]).

Focusing on the species number of the two extremes, i.e., the WG's and the DG's, our results were consistent with the literature reporting that the detectable proportion of the seed bank was relatively species-poor [3,49] (Table 2). Our results confirmed the literature reporting that there was only a marginal difference between the total species number of wetlands and of drier grasslands in favor of the latter (cf. circa 25 on average in European marshes, ca. 30 on average in European grasslands [1]; 25–26 in abandoned wet meadows dominated by *Carex acutiformis* [39], 23–29 in the 0–5 cm soil depth interval, and 18–19 in the 5–10 cm soil depth interval of resumed dry-mesophilous meadows dominated by *Brachypodium pinnatum* [9]). However, these results are influenced by the rate of species accumulation, which may vary from study to study.

Several references in the literature suggested that the seed bank of a typical wetland species is often persistent [14,50,51]. Moreover, some references in the literature suggested that the seed bank of a typical dry grassland species is seldom long-term persistent (through the example of perennials: Csontos [52,53]). According to the comparative analysis of Thompson et al. [16], persistent seed banks within the specialists of neither the wetland nor the dry grassland ran to higher than 40%. They also pointed out that there was only a negligible difference in persistence between the specialists of the two habitat types. Our results, which firstly showed that the transient species had the highest species number in all three grassland types, secondly showed that the proportion of the persistent species number to transient species number was slightly higher in the WG than in DG, and thirdly showed that the majority of the persistent species had high or medium moisture requirement, were only partially consistent with the results of Thompson et al. [16]. These results are in accordance with the theorem that seed bank persistence can be more or less determined by plant strategies.

The described feature of the seed bank, i.e., that the WG's seed bank was denser and more persistent than the DG's, may be related to soil conditions, in addition to species specificity. Soils with high moisture content are generally poor in O_2 [54], and in the case of hypoxia, they are more likely to have a seed-conserving effect [55]. In the case of anoxia, a seed-autolyzing effect may occur, but it is also unlikely to primarily strike hygrophytes [55]. As soils with high moisture content are less ideal for pathogenic fungi, their negative effect on seeds is less relevant [4,56]. In contrast, soils which do not have a particularly high moisture content, but are still fresh, are usually rich in O_2 [54] and favorable to pathogenic fungi [57]; thus, such soils can cause the multiplied reduction in the seed bank, as they provide adequate moisture and O_2 quantity for germination [55], and the seedlings and physiologically active seeds are more prone to pathogenic fungal infections [58,59].

It is known in the literature that certain species, due to their natural variability, may form different seed bank types under different environmental conditions [3,4,60]. Our own results have provided some examples of this intraspecific variability, but we will discuss this in more detail in another study.

4.3. Similarities between the Above-Ground Vegetation and the Soil Seed Bank from the Aspect of Recovery Potential in the Grassland Types

Our results that showed that the diversity of the vegetation exceeded that of the seed banks, are consistent with the outcomes of many studies [22,52]. The values that were obtained for the floristic similarity between the vegetation and the seed bank can be generally considered low, especially for the DG. In terms of similarity between the vegetation and the seed banks, the rankings of the WG and DG by magnitude were reversed, in comparison to those reported in the literature [1,8]. According to Bossuyt and Honnay [1], the Jaccard similarity between the vegetation and the seed banks was slightly higher in the case of drier grasslands (ca. 0.37 on average in Europe) than in the case of wetlands (ca. 0.35 on average in Europe). However, this ranking can be influenced, for example, by the date of sampling, the rate of species accumulation, the landscape history and the rate of stability/disturbance; therefore, it hardly serves as a basis for comparison. The fact that the highest similarity was found in the EG can be paralleled with the results of Lv et al. [61], who, when comparing the inner Mongolian typical steppe (i.e., fresher one), desert steppe (i.e., drier one) and the transition zone between them, found maximum similarity in the latter.

According to the literature, in most European habitat types, neither the dominant nor the rare endangered species of the vegetation form a persistent seed bank of remarkable density [3,9]. In the case of wetlands, however, it is not unprecedented that characteristic species of the vegetation, such as *Carex* spp., even if not definitely in the longer term, but at least in the short term, have a reasonable amount of seed bank [1,62]. Our results fit well with this tendency. In terms of recovery, the seed bank of the WG was considered to be the most valuable of the three studied grassland types, as some of the important species of the vegetation, including the dominant matrix species (*Carex acutiformis*) and a few endangered characteristic species (*Veronica longifolia*), were able to form a relatively dense and/or persistent seed bank (Table 3a,b). The value of the EG's seed bank that accumulated the seeds of matrix species and some less frequent but valuable hygrophyte species of the vegetation in high density, was degraded by the even higher density of the *Erigeron annuus* seeds (Table 3a,b).

Our results partially confirmed our hypothesis, as well as the accordant review of Kiss et al. [63], that generally considers the seed bank to be a crucial component of community resilience in wetlands. The above can be interpreted such that in the case of degradation, the spontaneous recovery of the WG from the seed bank is far from complete, but its seed bank supports an increase in diversity more than that of the DG. However, beyond five years from degradation, with the aging of the seed bank, the prospects for recovery will deteriorate considerably for the WG as well.

Since our examinations were only performed in a small locality, and thus may be affected by the inherent spatial autocorrelation of the system, our results can only be extrapolated to a limited extent. However, since our specific results for the studied location mostly followed presumable trends that were based on the literature, they provide a good basis for further investigation and verification. In order to explore generalizable trends, it would be worth repeating our study on a larger scale, in habitats that share similar climatic conditions, landscape history and environment.

5. Conclusions

Our local results, on the seed banks of the studied grassland types, can help to estimate the buffering capacity against climate change and anthropogenic activities of the hydrologically moderately predictable representatives of tall-sedge bed-like habitats, and also those of the more stable representatives of semi-dry grassland-like habitats, which are formed under the continental climate. Based on our results, we can more likely expect from the former that at least some of their characteristic species are able to form relatively dense and/or persistent seed banks, and are then able to partially recover. While we most likely cannot expect from the latter to maintain a quantitatively and qualitatively sufficient seed bank from which they are capable to spontaneously recover after degradation. In the light of the foregoing, the improving and scheduling of restoration management for similar habitat types can be helped. In the case of the drying out of a wet grassland with moderately predictable hydrology, it could be advisable to start water management within five years from drying out; however, if this period when the recovery would have been partially bufferable from the seed bank has already elapsed, the creation of a habitat type that is different from the original may be worth considering. In the case of the degradation of a more stable dry grassland, if natural seed rain cannot be expected, the restoration most likely cannot avoid the artificial introduction of the donor seed bank, which may become necessary even from the first year. At the same time, this also means that in the case of restoration attempts, within five years after destruction, it could be more rewarding to deal first with the former of the above two habitat types considering the exploitability of the services of the natural seed bank. Scheduling the restoration according to the above recognition, combined with monitoring the vegetation response by high spatial resolution airborne remote sensing [64,65], especially if performed by unmanned aerial vehicles [64], may substantially improve the efficiency of otherwise time-, labor-, cost- and resource-demanding interventions.

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Appendix A

Table A1. The relative soil moisture requirement system, according to Borhidi [31].

WB	Moisture Requirement Category
1	Plants of extremely dry habitats or bare rocks
2	Xero-indicators on habitats with long dry period
3	Xero-tolerants, but eventually occurring on fresh soils
4	Plants of semi-dry habitats
5	Plants of semi-humid habitats, under intermediate conditions
6	Plants of fresh soils
7	Plants of moist soils, not drying out and well aerated
8	Plants of moist soils tolerating short floods
9	Plants of wet, not well-aerated soils
10	Plants of frequently flooded soils
11	Water plants with floating or partly emergent leaves
12	Water plants, most wholly submerged in water

Table A2. Separability of the three predefined groups of quadrats along the slope, based on local soil and above-ground vegetation properties (linear discriminant analysis). Soil properties refer to the 0–10 cm soil depth interval.

Introduced Data Combination				Linear Discriminant Analysis			Difference
Dependent Var. = Groups		Independent Variables (norm.)		LD1 (58.5%)	LD2 (41.5%)	LD Groups	Target vs. LD Group
{G1 (6 quadrats)	~	Soil moisture content	→	−4.90	−0.85	G1 (6 quadrats)	±0 quadrat
G2 (18 quadrats)		+ Carbonate content		−0.57	−0.45	G2 (18 quadrats)	±0 quadrat
G3 (6 quadrats)}		+ Organic matter content		−1.86	6.81	G3 (6 quadrats)	±0 quadrat
		+ Water-soluble salt content		−2.11	−3.20		
		+ Consistency acc. to Arany		1.45	−0.97		
		+ pH determined in KCl		−0.63	−0.80		
		+ Vegetation cover		3.06	3.22		
		+ Species number		−2.51	−4.63		

Notation: G—group; norm.—dataset normalized into the interval of 0–1.

Table A3. Soil properties in the three grassland types with different water regimes.

	Wet Grassland Type, *N* = 6	Ecotone Grassland Type, *N* = 18	Semi-Dry Grassland Type, *N* = 6
	$\bar{X} \pm SD$	$\bar{X} \pm SD$	$\bar{X} \pm SD$
Soil moisture content (m/m%)			
October 2012	43.73 ± 6.80	33.67 ± 3.79	26.05 ± 1.40
November 2012	40.79 ± 8.26	33.24 ± 2.31	27.43 ± 1.53
October 2013	41.17 ± 4.02	33.83 ± 2.43	23.16 ± 1.82
Carbonate content (m/m%)	0.10 ± 0.00	5.39 ± 4.48	0.10 ± 0.00
Organic matter content (m/m%)	7.86 ± 0.64	5.63 ± 0.63	5.24 ± 0.43

Table A3. *Cont.*

	Wet Grassland Type, *N* = 6	Ecotone Grassland Type, *N* = 18	Semi-Dry Grassland Type, *N* = 6
	$\bar{X} \pm SD$	$\bar{X} \pm SD$	$\bar{X} \pm SD$
Water-soluble salt content (m/m%)	0.08 ± 0.01	0.07 ± 0.01	0.06 ± 0.02
Consistency according to Arany	83.83 ± 9.41	75.33 ± 4.83	69.33 ± 2.66
pH determined in KCl	6.46 ± 0.41	6.83 ± 0.34	6.04 ± 0.23

Standard: Hungarian standards [28–30].

Table A4. Identification of the seed bank type of the species in the three grassland types with different water regimes. The table contains only those species for which sufficient data were available in the given grassland type for reliable classification, i.e., based on the above-ground vegetation and/or the soil seed bank, the frequency of the species ≥3 in the grassland type; in the case of exclusive occurrence in the above-ground vegetation, the total cover of the species ≥1% in the grassland type; in the case of occurrence in the soil seed bank, the total seed number (total number of seedlings found) of the species ≥3 in the grassland type.

	WB	Presence in Vegetation	Presence in Seed Bank			ST
			0–5 cm		5–10 cm	
Wet grassland type, *N* = 6						
Alopecurus pratensis	6	+		–		T
Anagallis arvensis [!]	4	–	+	>	+	LP
Calystegia sepium	9	+		–		T
Carex acutiformis	9	+	+	>	–	T
Carex hirta	7	+	+	=	+	LP
Carex vulpine	8	+		–		T
Cirsium arvense [!]	4	+		–		T
Cirsium canum [!]	8	+		–		T
Colchicum autumnale [!]	6	+		–		T
Erigeron annuus [!]	7	+	+	>	+	SP
Filipendula ulmaria [!]	8	+		–		T
Filipendula vulgaris [!]	4	+		–		T
Galium boreale	8	+		–		T
Lathyrus pratensis	7	+		–		T
Lysimachia vulgaris	8	+		–		T
Lythrum salicaria	9	+	+	>	+	SP
Mentha aquatica	9	+		–		T
Ranunculus auricomus	6	+	+	>	–	T
Serratula tinctoria [!]	7	+		–		T
Silene flos-cuculi [!]	7	+	+	<	+	LP
Symphytum officinale	8	+		–		T
Thalictrum lucidum [!]	8	+	+	>	+	SP
Veronica longifolia	8	+	+	>	+	SP
Ecotone grassland type, *N* = 18						
Achillea collina	2	+	+	>	+	SP
Alopecurus pratensis	6	+		–		T
Anagallis arvensis [!]	4	–	+	=	+	LP
Arrhenatherum elatius	5	+		–		T
Calamagrostis epigejos [!]	5	+		–		T
Calystegia sepium	9	+		–		T
Carex acutiformis	9	+	+	>	+	SP
Carex hirta	7	+	+	≥	+	LP
Carex muricata ssp. pairae	5	+	+	>	+	SP

Table A4. *Cont.*

	WB	Presence in Vegetation	Presence in Seed Bank			ST
			0–5 cm		5–10 cm	
Cirsium arvense [!]	4	+		–		T
Colchicum autumnale [!]	6	+		–		T
Crepis biennis [!]	5	+		–		T
Dactylis glomerata	6	+		–		T
Erigeron annuus [!]	7	+	+	>	+	SP
Erigeron canadensis [!]	4	–	+	>	+	LP
Filipendula ulmaria [!]	8	+		–		T
Filipendula vulgaris [!]	4	+		–		T
Fragaria viridis	3	+		–		T
Galium verum	4	+		–		T
Inula salicina [!]	5	+		–		T
Juncus articulatus [!]	8	–	+	≤	+	LP
Lathyrus pratensis	7	+		–		T
Lathyrus tuberosus	4	+		–		T
Leucanthemum vulgare [!]	2	+	+	≥	+	LP
Lysimachia vulgaris	8	+		–		T
Lythrum salicaria	9	+	+	>	+	SP
Medicago lupulina	5	–	+	>	+	LP
Peucedanum alsaticum	3	+		–		T
Picris hieracioides [!]	4	+	+	>	–	T
Pimpinella saxifrage	3	+		–		T
Plantago major	6	+	+	>	+	SP
Plantago media	5	+	+	>	+	SP
Poa pratensis	6	+	+	<	+	LP
Pulmonaria mollis	5	+		–		T
Ranunculus auricomus	6	+		–		T
Ranunculus repens	8	+	+	<	+	LP
Salvia pratensis	3	+		–		T
Schedonorus pratensis	6	+		–		T
Serratula tinctoria [!]	7	+		–		T
Silene flos-cuculi [!]	7	+	+	<	+	LP
Solidago canadensis [!]	7	+	+	>	–	T
Stellaria media	5	–	+	<	+	LP
Symphytum officinale	8	+		–		T
Taraxacum officinale [!]	5	+	+	>	+	SP
Thalictrum lucidum [!]	8	+	+	>	+	SP
Trifolium campestre [!]	4	+		–		T
Trifolium pratense	6	+		–		T
Trisetum flavescens	6	+		–		T
Vicia hirsuta	3	+		–		T
Vicia sepium	5	+		–		T
Semi-dry grassland type, *N* = 6						
Achillea collina	2	+		–		T
Alopecurus pratensis	6	+		–		T
Brachypodium pinnatum	4	+		–		T
Carex hirta	7	+	+	≤	+	LP
Carex muricata ssp. pairae	5	–	+	>	+	SP
Carex praecox	3	+		–		T
Colchicum autumnale [!]	6	+		–		T
Dactylis glomerata	6	+		–		T
Elytrigia repens	5	+		–		T
Erigeron annuus [!]	7	–	+	>	+	SP
Festuca stricta ssp. sulcata	3	+		–		T
Filipendula vulgaris [!]	4	+		–		T
Galium verum	4	+		–		T
Inula salicina [!]	5	+		–		T
Lathyrus pratensis	7	+		–		T

Table A4. *Cont.*

	WB	Presence in Vegetation	Presence in Seed Bank			ST
			0–5 cm		5–10 cm	
Peucedanum alsaticum	3	+		–		T
Peucedanum cervaria	2	+		–		T
Poa pratensis	6	+	+	>	–	T
Ranunculus acris	7	+		–		T
Salvia pratensis	3	+		–		T
Serratula tinctoria !	7	+		–		T
Silene latifolia	4	–	+	>	+	LP
Silene otites	2	+	+	>	–	T
Stellaria media !	5	–	+	<	+	LP
Trifolium campestre !	4	+		–		T
Trifolium montanum	3	+		–		T
Verbascum phoeniceum !	2	+	+	>	–	T
Vicia cracca	4	+		–		T

Notation: WB—relative soil moisture requirement according to the system of Borhidi [31]; for the resolution of its category denotations, see Appendix A, Table A1. ST—seed bank type referring to the 3-category system of Thompson [43], where "T" means transient, "SP" means short-term and "LP" means long-term persistent; species names labelled with "!" in superscript indicate species capable of anemochory, according to Csontos et al. [44]. Nomenclature: the scientific names of the species follow the nomenclature of the Euro+Med [33].

References

1. Bossuyt, B.; Honnay, O. Can the seed bank be used for ecological restoration? An overview of seed bank characteristics in European communities. *J. Veg. Sci.* **2008**, *19*, 875–884. [CrossRef]
2. Kiss, R. The role of soil seed bank in restoration and dynamics of Hungarian plant communities—A review of Hungarian seed bank research. *Kitaibelia* **2016**, *21*, 116–135. [CrossRef]
3. Thompson, K.; Bakker, J.P.; Bekker, R.M. *Soil Seed Banks of North West Europe: Methodology, Density and Longevity*; Cambridge University Press: Cambridge, UK, 1997.
4. Abedi, M.; Bartelheimer, M.; Poschlod, P. Effects of substrate type, moisture and its interactions on soil seed survival of three *Rumex* species. *Plant Soil* **2014**, *374*, 485–495. [CrossRef]
5. Bakker, J.P.; Poschlod, P.; Strykstra, R.J.; Bekker, R.M.; Thompson, K. Seed banks and seed dispersal: Important topics in restoration ecology. *Acta Bot. Neerl.* **1996**, *45*, 461–490. [CrossRef]
6. Thompson, K.; Band, S.R.; Hodgson, J.G. Seed size and shape predict persistence in soil. *Funct. Ecol.* **1993**, *7*, 236–241. [CrossRef]
7. Bekker, R.M.; Bakker, J.P. Seed traits: Essential for understanding seed longevity. *Asp. Appl. Biol.* **2003**, *69*, 1–9.
8. Hopfensperger, K.N. A review of similarity between seed bank and standing vegetation across ecosystems. *Oikos* **2007**, *116*, 1438–1448. [CrossRef]
9. Valkó, O.; Török, P.; Vida, E.; Arany, I.; Tóthmérész, B.; Matus, G. The role of soil seed banks in restoration of two hay meadows. *Természetvédelmi Közlemények* **2009**, *15*, 147–159, (In Hungarian with English summary).
10. Ma, M.; Zhou, X.; Ma, Z.; Du, G. Composition of the soil seed bank and vegetation changes after wetland drying and soil salinization on the Tibetan Plateau. *Ecol. Eng.* **2012**, *44*, 18–24. [CrossRef]
11. Simmering, D.; Waldhardt, R.; Otte, A. Quantifying determinants contributing to plant species richness in mosaic landscapes: A single- and multi-patch perspective. *Landsc. Ecol.* **2006**, *21*, 1233–1251. [CrossRef]
12. Bakker, J.P. *Nature Management by Grazing and Cutting: On the Ecological Significance of Grazing and Cutting Regimes Applied to Restore Former Species-rich Grassland Communities in the Netherlands (Geobotany 14)*; Kluwer Academic Publishers: Dordrecht, The Netherlands, 1989. [CrossRef]
13. Wellstein, C.; Otte, A.; Waldhardt, R. Seed bank diversity in mesic grasslands in relation to vegetation type, management and site conditions. *J. Veg. Sci.* **2007**, *18*, 153–162. [CrossRef]
14. Leck, M.A.; Schütz, W. Regeneration of *Cyperaceae*, with particular reference to seed ecology and seed banks. *Perspect. Plant Ecol. Evol. Syst.* **2005**, *7*, 95–133. [CrossRef]
15. Ludewig, K.; Zelle, B.; Eckstein, R.L.; Mosner, E.; Otte, A.; Donath, T.W. Differential effects of reduced water potential on the germination of floodplain grassland species indicative of wet and dry habitats. *Seed Sci. Res.* **2014**, *24*, 49–61. [CrossRef]
16. Thompson, K.; Bakker, J.P.; Bekker, R.M.; Hodgson, J.G. Ecological correlates of seed persistence in soil in the north-west European flora. *J. Ecol.* **1998**, *86*, 163–169. [CrossRef]
17. Baker, H.G. Seed weight in relation to environmental conditions in California. *Ecology* **1972**, *53*, 997–1010. [CrossRef]
18. Leishman, M.R.; Westoby, M. The role of seed size in seedling establishment in dry soil conditions—Experimental evidence from semi-arid species. *J. Ecol.* **1994**, *82*, 249–258. [CrossRef]

19. Tautenhahn, S.; Heilmeier, H.; Götzenberger, L.; Klotz, S.; Wirth, C.; Kühn, I. On the biogeography of seed mass in Germany—Distribution patterns and environmental correlates. *Ecography* **2008**, *31*, 457–468. [CrossRef]
20. Bekker, R.M.; Bakker, J.P.; Gradin, U.; Kalamees, P.; Milberg, P.; Poschlod, P.; Thompson, K.; Willems, H. Seed size, shape and vertical distribution in the soil: Indicators of seed longevity. *Funct. Ecol.* **1998**, *12*, 834–842. [CrossRef]
21. Csontos, P. *Methods for Studying the Natural Seed Bank (Synbiologia Hungarica 4)*; Scientia Kiadó: Budapest, Hungary, 2001. (In Hungarian)
22. Csontos, P. Advances in studying soil seed bank and other seed-related ecological questions, concerning to the Hungarian flora. *Kanitzia* **2010**, *17*, 77–110, (In Hungarian with English summary).
23. Csontos, P.; Kalapos, T.; Tamás, J. Seed trait databases—Ecological applications. *J. Landsc. Ecol.—Tájökológiai Lapok* **2013**, *11*, 335–339, (In Hungarian with English summary).
24. Dövényi, Z. (Ed.) *Inventory of Microregions in Hungary*, 2nd ed.; MTA Geographical Research Institute: Budapest, Hungary, 2010. (In Hungarian)
25. Schellenberger, J. Soil Seed Bank Examinations in Grassland Types with Different Water Regime. Ph.D. Thesis, Hungarian University of Agriculture and Life Sciences, Gödöllő, Hungary, 2021. (In Hungarian with English summary).
26. Ter Heerdt, G.N.J.; Verweij, G.L.; Bekker, R.M.; Bakker, J.P. An improved method for seed bank analysis: Seedling emergence after removing the soil by sieving. *Funct. Ecol.* **1996**, *10*, 144–151. [CrossRef]
27. Csontos, P. Seed bank ecology II. Techniques for estimation of seed banks in soil samples and comparison of methods. *Acta Agronomica Óváriensis* **2000**, *42*, 133–150, (In Hungarian with English summary).
28. *MSZ-08-0210:1977*; Testing Organic Carbon Content in Soils. Hungarian Standards Institution: Budapest, Hungary, 1977. (In Hungarian)
29. *MSZ-08-0205:1978*; Determination of Physical and Hydrophysical Properties of Soils. Hungarian Standards Institution: Budapest, Hungary, 1978. (In Hungarian)
30. *MSZ-08-0206-2:1978*; Evaluation of Some Chemical Properties of the Soil: Laboratory Tests (pH Value, Phenolphtaleine Alkalinity Expressed in Soda, All Water Soluble Salts, Hydrolite (y_1-Value) and Exchanging Acidity (y_2-Value)). Hungarian Standards Institution: Budapest, Hungary, 1978. (In Hungarian)
31. Borhidi, A. Social behaviour types, the naturalness and relative ecological indicator values of the higher plants in the Hungarian Flora. *Acta Bot. Hung.* **1995**, *39*, 97–181.
32. Horváth, F.; Dobolyi, Z.K.; Morschhauser, T.; Lőkös, L.; Karas, L.; Szerdahelyi, T. *Hungarian FLORA Database 1.2: List of Taxa and Relevant Attributes*; FLÓRA Workgroup of MTA Institute of Ecology and Botany–MTM Department of Botany: Vácrátót, Hungary, 1995; (In Hungarian with English summary).
33. Euro+Med (2006–): Euro+Med PlantBase—The Information Resource for Euro-Mediterranean Plant Diversity. Available online: http://ww2.bgbm.org/EuroPlusMed/ (accessed on 1 January 2022).
34. Hammer, Ø.; Harper, D.A.T.; Ryan, P.D. PAST: Paleontological statistics software package for education and data analysis. *Palaeontol. Electron.* **2001**, *4*, 1–9.
35. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2017.
36. Maechler, M.; Rousseeuw, P.; Struyf, A.; Hubert, M.; Hornik, K. *Cluster: Cluster Analysis Basics and Extensions. R Package Version 2.0.8*; R Foundation for Statistical Computing: Vienna, Austria, 2019.
37. Venables, W.N.; Ripley, B. *Modern Applied Statistics with S*, 4th ed.; Springer: New York, NY, USA, 2002. [CrossRef]
38. Valkó, O.; Török, P.; Tóthmérész, B.; Matus, G. Restoration potential in seed banks of acidic fen and dry-mesophilous meadows: Can restoration be based on local seed banks? *Restor. Ecol.* **2011**, *19*, 9–15. [CrossRef]
39. Jensen, K. Species composition of soil seed bank and seed rain of abandoned wet meadows and their relation to aboveground vegetation. *Flora* **1998**, *193*, 345–359. [CrossRef]
40. Bölöni, J.; Molnár, Z.; Kun, A. (Eds.) *Habitats of Hungary: Description and Determinant of Vegetation Types in Hungary: ÁNÉR 2011*; MTA Institute of Ecology and Botany: Vácrátót, Hungary, 2011. (In Hungarian)
41. Davies, C.E.; Moss, D.; Hill, M.O. *EUNIS Habitat Classification Revised 2004. Report to the EEA European Topic Centre on Nature Protection and Biodiversity*; European Economic Area: Copenhagen, Denmark, 2004.
42. Zar, J.H. *Biostatistical Analysis*, 5th ed.; Prentice Hall: Upper Saddle River, NJ, USA, 2010.
43. Thompson, K. Seed persistence in soil. In *Methods in Comparative Plant Ecology: A Laboratory Manual*; Hendry, G.A.F., Grime, J.P., Eds.; Chapman and Hall: London, UK, 1993; pp. 199–202.
44. Csontos, P.; Tamás, J.; Tobisch, T. Presentation of seed dispersal database of the Hungarian Flora through analytical examples: Evaluation of Social Behaviour Types. In *Botanical Researches in Hungary at the Millennium: Studies in Honour of Attila Borhidi's 70th Birthday*; Salamon-Albert, É., Ed.; PTE Department of Botany: Pécs, Hungary, 2002; pp. 557–569. (In Hungarian)
45. Hungarian Ministry of Environmental Protection. 13/2001. (V. 9.) KöM decree on protected and specially protected plant and animal species, the range of specially protected caves and the publication of species of plant and animal species of conservation importance in the European Community. *Magyar Közlöny* **2001**, *53*, 3446–3511. (In Hungarian)
46. Labrada, R. (Ed.) *Weed Management for Developing Countries (FAO Plant Production and Protection Paper 120, Addendum 1)*; Food and Agriculture Organization of the United Nations: Rome, Italy, 2003.

47. Wang, Y.; Jiang, D.; Toshio, O.; Zhou, Q. Recent advances in soil seed bank research. *Contemp. Probl. Ecol.* **2013**, *6*, 520–524. [CrossRef]
48. Thompson, K. The functional ecology of seed banks. In *Seeds: The Ecology of Regeneration in Plant Communities*; Fenner, M., Ed.; CAB International: Wallingford, UK, 1992; pp. 231–258. [CrossRef]
49. Thompson, K.; Grime, J.P. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *J. Ecol.* **1979**, *67*, 893–921. [CrossRef]
50. Harper, J.L. *Population Biology of Plants*; Academic Press: London, UK, 1977.
51. Brock, M.A.; Nielson, D.L.; Shiel, R.J.; Green, J.D.; Langley, J.D. Drought and aquatic community resilience: The role of eggs and seeds in sediments of temporary wetlands. *Freshw. Biol.* **2003**, *48*, 1207–1218. [CrossRef]
52. Csontos, P. Fundamentals of Seed Bank Ecology, the Seed Ecological Study of the Hungarian Flora. D.Sc. Thesis, Hungarian Academy of Sciences, Budapest, Hungary, 2006. (In Hungarian).
53. Csontos, P. Seed longevity studies on species of weedy places, dry grasslands and forests. *Magy. Gyomkutatás Technol.* **2006**, *7*, 101–112, (In Hungarian with English summary).
54. Oomes, M.J.M.; Kuikman, P.J.; Jacobs, F.H.H. Nitrogen availability and uptake by grassland in mesocosms at two water levels and two water qualities. *Plant Soil* **1997**, *192*, 249–259. [CrossRef]
55. Bekker, R.M.; Oomes, M.J.M.; Bakker, J.P. The impact of groundwater level on soil seed bank survival. *Seed Sci. Res.* **1998**, *8*, 399–404. [CrossRef]
56. Albrecht, H.; Auerswald, K. Arable weed seedbanks and their relation to soil properties. *Asp. Appl. Biol.* **2003**, *69*, 11–20.
57. Pakeman, R.J.; Small, J.L.; Torvell, L. Edaphic factors influence the longevity of seeds in the soil. *Plant Ecol.* **2012**, *213*, 57–65. [CrossRef]
58. Kirkpatrick, B.L.; Bazzaz, F.A. Influence of certain fungi on seed germination and seedling survival of four colonizing annuals. *J. Appl. Ecol.* **1979**, *16*, 515–527. [CrossRef]
59. Chambers, J.C.; MacMahon, J.A. A day in the life of a seed: Movements and fates of seeds and their implications for natural and managed systems. *Annu. Rev. Ecol. Syst.* **1994**, *25*, 263–292. [CrossRef]
60. Kaiser, T.; Pirhofer-Walzl, K. Does the soil seed survival of fen-meadow species depend on the groundwater level? *Plant Soil* **2015**, *387*, 219–231. [CrossRef]
61. Lv, Y.; Shen, M.; Meng, B.; Zhang, H.; Sun, Y.; Zhang, J.; Chang, L.; Li, J.; Yi, S. The similarity between vegetation and soil seed bank of grasslands in Inner Mongolia, China: Implications for the asymmetric response of productivity to precipitation. *Plants* **2021**, *10*, 1890. [CrossRef]
62. Matus, G.; Verhagen, R.; Bekker, R.M.; Grootjans, A.P. Restoration of the *Cirsio dissecti-Molinietum* in The Netherlands: Can we rely on soil seed banks? *Appl. Veg. Sci.* **2003**, *6*, 73–84. [CrossRef]
63. Kiss, R.; Deák, B.; Török, P.; Tóthmérész, B.; Valkó, O. Grassland seed bank and community resilience in a changing climate. *Restor. Ecol.* **2018**, *26*, S141–S150. [CrossRef]
64. Sun, Y.; Yi, S.; Hou, F. Unmanned aerial vehicle methods makes species composition monitoring easier in grasslands. *Ecol. Indic.* **2018**, *95*, 825–830. [CrossRef]
65. Fehérváry, I.; Kiss, T. Automatised identification of vegetation types on a floodplain area based on airborne LIDAR survey. *J. Landsc. Ecol.—Tájökológiai Lapok* **2020**, *18*, 127–140. (In Hungarian with English Summary)