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Environmental factors driving seed bank diversity in alkali grasslands

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ABSTRACT

For an effective conservation and management in grasslands it is essential to understand mechanisms sustaining biodiversity. To gain knowledge is especially crucial in stressed grasslands harbouring a unique flora and fauna, like alkali grasslands. Aboveground vegetation, seed bank and environmental factors were studied in three stands of the following alkali grassland types: (i) *Artemisia* dry alkali grasslands at highest elevations; (ii) *Puccinellia* high and (iii) *Puccinellia* low grasslands at medium to low elevations, and (iv) *Juncus* wet alkali grasslands at the lowest elevations. We tested the following hypotheses: (i) Seed bank species diversity and density are the highest in the most stressed grassland types, where regeneration by seeds could have a major importance in sustaining vegetation diversity. (ii) Seed bank density of hygrophytes increases with decreasing elevation, because the cover of hygrophytes in the vegetation increases with decreasing elevation. The mean seed bank density ranged from 30,104 up to 51,410 seeds/m^2, which is higher than in most dry grasslands. Both the lowest seed bank density and diversity were detected in the most stressed *Puccinellia* high grasslands; *Spergularia salina* was the only abundant seed bank species (possessing at least 1000 seeds/m^2). These results not supported our first hypothesis. We detected the highest seed densities of almost all hygrophyte species in the lowest-elevated *Juncus* grasslands. But, we did not find a significant monotonous correlation between elevation and the overall hygrophyte seed bank density; because most of the hygrophyte species were missing from the seed bank at the medium-elevated, but most saline *Puccinellia* grasslands. Thus, our results only partly supported the second hypothesis. In total we detected more species in the seed bank than in the aboveground vegetation which emphasises that seed bank plays an important role in sustaining the diversity of alkali grasslands. However, characteristic graminoids possessed no considerable seed bank, except for *Juncus compressus* (up to 38,619 seeds/m^2). We can conclude that persistence and establishment of most alkali grassland species are not supported by the local persistent seed bank.

1. Introduction

Conservation of grassland biodiversity is an urgent task nowadays, because grasslands are in decline and they contribute with a significant part to the biodiversity of Europe, harbouring a very diverse flora and fauna of conservation interest at different spatial scales (Donath et al., 2007; Kovács-Hostyánszky et al., 2011; Reitalu et al., 2013; Wilson et al., 2012). To achieve an effective conservation and management of grassland biodiversity it is essential to understand mechanisms and ecosystem functions sustaining natural grassland communities from local up to landscape scales (Lindborg et al., 2008; Drobnik et al., 2011; Zeiter et al., 2013). Understanding ecosystem functions responsible for grassland biodiversity also supports the planning and implementation of grassland restoration actions (Török et al., 2011a; Prach et al., 2013). To gain knowledge is especially crucial in environmentally stressed grasslands which harbour a unique flora and fauna like alkali grasslands (Kelemen et al., 2013).

There are contrasting views regarding the role of persistent seed bank in sustaining biodiversity of stressed communities. Several authors argue that in stressful conditions instead of sexual reproduction a higher investment in clonal spread is necessary, which suggest that seed bank may plays a subordinate role in these communities (Chang et al., 2001; Bossuyt and Honnay, 2008). However, the seed bank can have a crucial importance in vegetation dynamics in stressed communities as found by others (see Fenner and Thompson, 2005). Persistent seed bank allows species to bridge temporally unsuitable habitat conditions for germination

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and establishment (Bossuyt and Honnay, 2008). The role of persistent seed bank was found to be especially important in salt-affected communities, where highly saline conditions generally hamper seed germination, resulting in the formation of persistent seed bank (Ungar, 1991). Soil salinity is found to be one of the major factors determining seed germination either osmotically or through a specific ion-effect in salt-affected communities (Egan and Ungar, 2000).

Several authors studied the seed bank of salt-affected communities in relation with aboveground vegetation, soil salinity or water regime. The majority of these studies focused on inland (e.g. Badger and Ungar, 1994; Egan and Ungar, 2000) or coastal salt marshes (Chang et al., 2001; Shumway and Bertness, 1992), seashore meadows (Jutila, 1998), Mediterranean salt grasslands (Maranón, 1998) or salt deserts (Khan, 1993), but such studies in inland alkali grassland's seed bank are still lacking.

Inland alkali grasslands are of special interest of the Natura 2000 network, and are included as "Pannonic salt steppes and salt marshes (1530)". Pannonic alkali grasslands are one of the best preserved grassland habitats in Europe typical for the Pannonian biogeographical region (Török et al., 2011b). They harbour several plants and animal species listed in Annex I and Annex II like *Cirsium brachycephalum* or *Gortyna borelii lunata*. Alkali grasslands are present at sites with moderate to high salt content and high springtime groundwater levels in continental climate. Alkali grasslands are traditionally used as extensively managed pastures, because their poor soil quality and fluctuating water regime makes them unsuitable for intensive agriculture and forestry (Molnár and Borhidi, 2003; Török et al., 2011a). The plant life in alkali grasslands is influenced by several stress factors like the (i) high osmotic pressure, (ii) ion-toxicity, (iii) unbalanced and fluctuating ion concentrations, (iv) unfavourable soil structure, (v) suboptimal soil pH and (vi) nutrient deficiency (Füzy et al., 2010). Elevation and soil pH were found to be important factors affecting vegetation composition in salt-affected communities (Davy et al., 2011; Wanner et al., 2013). In line with the uneven pattern of these stressors, different types of alkali grasslands are situated along an elevation gradient where even a few centimetre difference in elevation results in the formation of a different aboveground vegetation composition (Kelemen et al., 2013).

In the present study we provide a detailed analysis of seed bank composition of four types of alkali grasslands in relation with aboveground vegetation and some crucial environmental parameters (elevation, salinity, soil water content, soil organic matter and soil water capacity). We aimed at the analysis of environmental parameters in relation to the species composition and diversity of aboveground vegetation and soil seed bank in the studied alkali grassland types. We specifically tested the following hypotheses: (i) Seed bank species diversity and density are the highest in the most stressed grassland types where regeneration by seeds could have a major importance in sustaining vegetation diversity (Hopfensperger, 2007). (ii) Seed bank density of hygrophytes increases with decreasing elevation, because the cover of hygrophytes in the vegetation increases with decreasing elevation (Jutila, 2002). Our ultimate goal was to analyze the effects of environmental parameters on the species composition and density of the soil seed bank.

2. Materials and methods

2.1. Study area

Our study area is located in a mosaic alkali landscape in Nagy-Szik, Hortobágy, near the town Balmazújváros in East-Hungary (47° 35′ N and 20° 30′ E). The region is characterized by a moderately continental climate. The mean annual temperature is 9.5 C, while the mean annual precipitation is 550 mm with high among-year variations. The vegetation of the region is characterized by alkali grasslands, with scattered alkali marshes on the lowest and loess grassland patches on the highest elevations. The whole study area is traditionally managed by moderate cattle and sheep grazing. Meadow solonetz soils with a salt accumulation zone in deeper soil layers are typical in the study area. The selection of studied grassland types was based on Kelemen et al. (2013) study; we selected the most widespread alkali grassland types along an elevation gradient. The difference between highest and lowest elevated plot was only 30 cm. We studied the aboveground vegetation, seed bank and environmental factors in each of the three stands of a given of alkali grassland type: (i) *Artemisia* dry alkali grasslands at highest elevations; (ii) *Puccinellia* high and (iii) *Puccinellia* low grasslands at medium to low elevations, and (iv) *Juncus* wet alkali grasslands at the lowest elevations.

2.2. Sampling setup

2.2.1. Analysis of environmental variables

In three stands of each grassland type we designated five 1 m × 1 m permanent plots in early spring, 2009. We measured the elevation (a.s.l.) in the centre of each plot with 1–3 cm accuracy (TOPCON GRS-1). We collected five soil cores (4-cm in diameter, 10-cm in depth) with a soil corer in late April 2010 for soil analysis. To determine soil moisture, we collected wet soil in plastic bags. The weight of the collected wet soil was measured with a tare balance immediately after transportation into laboratory. Soil samples were then air-dried at room temperature. The weight of air-dried samples was measured with 0.01 g accuracy. Soil water content was calculated from the differences between the weight of wet and air-dried samples. Soil solution was prepared for pH and conductivity measurements. From the wet soil 6.0 g samples were put into plastic beakers and filled with 50 ml deionised water.

The pH was measured using a digital type Testo 206 (Testo AG, Germany). Salinity was expressed by soil electrical conductivity (EC_a), which was measured with Soil Test EC & Temp HI98331, Mauritius. Soil organic matter (SOM) was assessed with loss on ignition (LOI) method. Air-dried samples (0.5 g) were dried at 105 °C overnight. Then, samples were weighted and then combusted at 550 °C for 5 h in a muffle furnace (Nabertherm L5/C6, Germany). After combustion, samples were cooled in desiccators and weighted again with an analytical balance (type SARTORIUS 6MBH Germany). Soil organic matter (SOM) was calculated using the following equation: $LOI_{550} = ((DW_{105} - DW_{550})/DW_{105})*100$; where "$LOI_{550}$" means the soil organic matter, "DW_{105}" the soil dry weight at 105 °C, and "DW_{550}" the soil dry weight at 550 °C (MSZ-15296:1999). Soil water capacity was determined using Arany-type plasticity index (P_A). In a mortar 100 g air-dried soil was put and it was mixed with deionised water until a homogeneous paste was formed. After the deionised water was added drop-wise till the upper limit of plasticity was realized by the so-called thread proof (MSZ-08 0205:1978). Arany-type plasticity index was calculated by the following equation: $P_A = 100 * V/M$, where "V" is the amount of deionised water used, while "M" is the weight of the soil. The measured soil water capacity can be assigned to the following physical soil categories: $P_A < 25$ coarse sand, $P_A = 25–30$ sand, $P_A = 31–37$ sandy loam, $P_A = 38–42$ loam, $P_A = 43–50$ clay loam, $P_A = 51–60$ clay and $P_A > 60$ heavy clay soils.

2.2.2. Vegetation and seed bank sampling

The percentage cover of vascular plants was recorded in each plot in June 2009. Soil seed bank was analysed with the seedling emergence method. Three soil cores (4-cm in diameter and 10-cm in depth; 126 cm^3/core) per plot were drilled after snowmelt

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Table 1
Enviromental and site characteristics of grasslands (mean ± SD). Significant differences between the studied grassland types were indicated using superscripted letters (one-way ANOVA and Tukey test). Notations: AG = *Artemisia* grasslands; PHG = *Puccinellia* high grasslands; PLG = *Puccinellia* low grasslands; JG = *Juncus* grasslands.

	$F_{3,12}$	*p*	AG	PHG	PLG	JG
Elevation (m a.s.l.)	10.970	**	89.79 ± 0.03^{c}	89.74 ± 0.05^{bc}	89.67 ± 0.04^{ab}	89.61 ± 0.05^{a}
pH	40.862	***	7.40 ± 0.04^{b}	7.75 ± 0.02^{c}	7.56 ± 0.18^{bc}	6.91 ± 0.06^{a}
Soil electrical conductivity (mS/cm)	7.666	**	2.13 ± 0.56^{ab}	2.80 ± 0.41^{b}	1.65 ± 0.65^{a}	0.98 ± 0.12^{a}
Soil organic matter (%)	15.124	***	6.79 ± 0.17^{a}	5.67 ± 1.05^{a}	6.58 ± 0.28^{a}	8.95 ± 0.57^{b}
Soil water content (%)	8.575	**	22.65 ± 2.49^{b}	14.80 ± 3.40^{a}	18.39 ± 0.82^{ab}	24.37 ± 2.76^{b}
Soil water capacity (cm^3)	7.304	*	53.99 ± 1.52^{ab}	46.66 ± 6.58^{a}	49.65 ± 2.64^{a}	60.01 ± 1.62^{b}

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

in 2010 (altogether 15 cores per stand; 180 cores in total). Cores from the same plot were pooled and samples were concentrated by sieving using the method of ter Heerdt et al. (1996). Vegetative organs were separated by washing over a coarse sieve (3-mm mesh size), while seed-free fine soil components were washed out using a 0.2-mm-fine mesh. Concentrated samples were spread in a 3–4-mm-thick layer on trays, formerly filled with 5-cm of steam-sterilized potting soil. Trays were placed under natural light in a greenhouse and watered regularly from April till October. Seedlings were regularly counted, identified, then removed or transplanted and grown till identification. In early July, when no seedlings emerged, watering was stopped, and the dried sample layers crumbled and turned. In late August, watering was re-started and continued until the early days of November. Accidental airborne seed contamination was monitored in sample-free control trays filled with steam-sterilized potting soil.

2.3. Data processing and analysis

Seedlings of *Juncus compressus* and *J. gerardii* were pooled as *Juncus compressus* (uppermost of the flowering *Juncus* specimens of the pooled group both in the field and seed bank were *J. compressus*); and *Typha angustifolia* and *T. latifolia* seedlings were pooled as *Typha* spp. in all analyses. Species were categorized as halophytes and hygrophytes based on indicator values for soil salt content (S) and humidity (W) of Ellenberg et al. (1991), adapted to local conditions by Borhidi (1995) as SB and WB values. Species having WB scores higher than 6 were considered as hygrophytes, and species having SB scores higher than 6 were considered as halophytes. Seed bank data from the same stands were pooled to decrease sample heterogeneity (15 cores, total volume 1885 cm^3).

To compare physical and chemical soil parameters, vegetation and seed bank characteristics between grassland types, one-way ANOVA was used on mean scores calculated for each grassland stand (altogether 3 averages for each grassland type). To indicate significant differences between grassland types Tukey HSD test was used (Zar, 1999). Univariate statistics were calculated using SPSS 17.0 statistical package. The diversity of vegetation and seed bank was calculated using ln based Shannon diversity. The similarities in species composition of the vegetation and seed bank were expressed using Sørensen similarity (Legendre and Legendre, 1998). The correlation between species composition of vegetation and seed bank composition and environmental parameters (elevation, salinity, soil organic matter, soil water content and soil water capacity) was displayed by a CCA calculated using CANOCO 4.5 package (ter Braak and Šmilauer, 2002). The statistical significance of the CCA was tested using a Monte Carlo unrestricted permutation test under full model with 9999 random permutations (Lepš and Šmilauer, 2003). To analyse correlations between vegetation and seed bank characteristics and environmental parameters Spearman rank-correlation was used (Zar, 1999).

3. Results

3.1. Effects of environmental variables on vegetation and seed bank composition

We detected the highest scores for soil water capacity, soil organic matter and soil water content, and also the lowest scores for salinity in *Juncus* grasslands. We detected the highest salinity scores and also the lowest scores for soil water capacity, soil organic matter and soil water content in *Puccinellia* high grasslands (Table 1). These results were clearly presented also by the CCA ordination, where data points of vegetation and seed bank of different grassland types were separated similarly along the mentioned environmental variables (Fig. 1). We found that salinity did not correlate significantly with Shannon diversity of the vegetation and that of the seed bank. Soil water content did not have a significant effect on the Shannon diversity of vegetation and seed banks. The cover and species richness of hygrophytes in the aboveground vegetation decreased significantly with increasing elevation (Spearman rank correlation, $r = -0.622$, $p = 0.029$ for cover scores and $r = -0.765$, $p = 0.003$ for species richness, respectively). Elevation did not have a significant effect on total- and hygrophyte seed density.

3.2. Vegetation and seed bank of the studied grassland types

We found altogether 39 species in the aboveground vegetation (25 species in *Artemisia* grasslands, 23 in *Puccinellia* high grasslands, 29 in *Puccinellia* low grasslands, and 28 in *Juncus* grasslands, respectively). We detected altogether 50 species in the seed bank (26 species in *Artemisia* grasslands, 17 in *Puccinellia* high grasslands, 28 in *Puccinellia* low grasslands, and 36 in *Juncus* grassland, respectively). 27 species were present both in vegetation and seed bank, 12 species were found only in the vegetation and 23 species were only found in the seed bank. The most abundant species in the vegetation and seed bank are listed in Tables A1–A3. The mean scores of Sørensen similarity of vegetation and seed bank ranged from 0.37 in *Puccinellia* high grasslands to 0.47 in *Juncus* grasslands (Table 2).

The CCA ordination revealed a clear distinction both for the vegetation and seed bank between the studied grassland types (Fig. 1). The Monte Carlo permutation tests indicated that the CCA both for the vegetation and seed bank was significant (9999 random permutations, $p = 0.0001$, $F = 7.365$ and 4.141, respectively). No significant differences were found between Shannon diversity scores of the grassland types neither in the vegetation nor in the seed bank. However, the highest vegetation and the lowest seed bank diversity scores were typical in the two types of *Puccinellia* grasslands (Table 2). The lowest seed density scores were found in *Puccinellia* high grasslands (Table 2). We detected the highest seed density scores in *Juncus* grasslands and the highest seed bank diversity scores in *Artemisia* and *Juncus* grasslands (Table 2).

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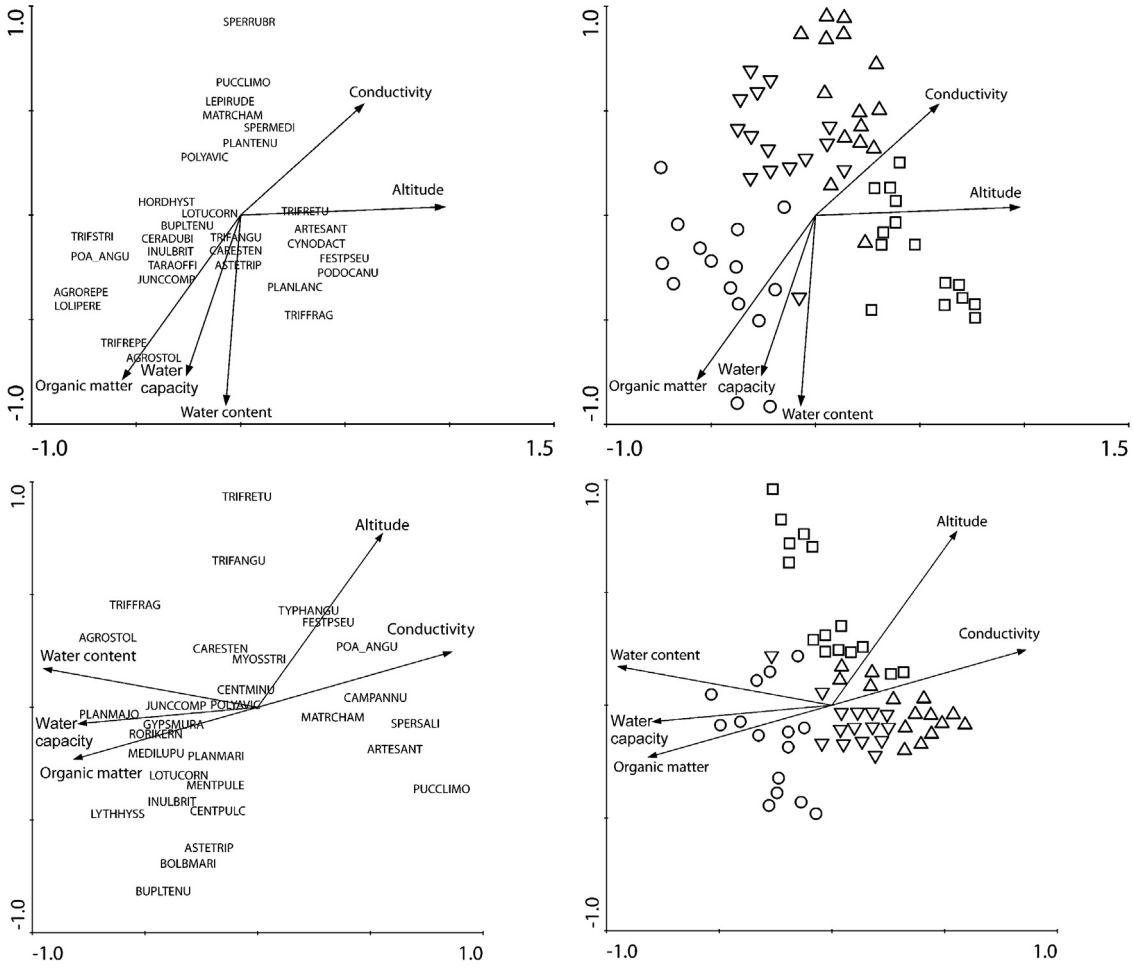

Fig. 1. The relation of environmental variables to (a,b) vegetation and (c,d) seed bank composition displayed by CCA. Main matrix consisted for vegetation cover scores (%) and for seed bank seedling numbers. First (x) and second (y) CCA axes are displayed; the cumulative species variances of the first and second axis were 20.7 and 37.3 for vegetation, and 21.4 and 26.3 for seed bank, respectively. Notations: *Artemisia* grasslands – Δ; *Puccinellia* high grasslands – ▽; *Puccinellia* low grasslands – □; *Juncus* grasslands – ◯, conductivity = soil electrical conductivity, organic matter = soil organic matter, water content = soil water content, water capacity = soil water capacity (for mean scores see Table 1). Soil electrical conductivity and pH were highly correlated; thus, only soil electrical conductivity was used in the calculation of the CCA. The most frequent 30 species are denoted by a combination of 4 letters of genus and 4 letters of species names like the following example: SPERSALI = *Spergularia salina*.

The seed bank of *Puccinellia* high grasslands was composed of a few species, and the only species with seed densities higher than 1000 seeds/m^2 were *Spergularia salina* and *Juncus compressus* (Fig. 1, Table A2). The seeds of *Spergularia salina* contributed by 71.5% up to 81.8% to the total seed bank in *Puccinellia* high grasslands. Other halophytes either had the highest seed densities in *Puccinellia* high and low grasslands (like *Camphorosma annua* and *Matricaria chamomilla*) or had no considerable seed bank (like *Puccinellia limosa* or *Hordeum hystrix*).

Out of the species with the highest cover in aboveground vegetation, *Juncus compressus* was the only species with considerable seed bank (Tables A2 and A3). We found that *Juncus compressus* was present in considerable densities in the seed bank of every studied grassland types, having especially high density in *Artemisia* and *Juncus* grasslands contributing the 35.7–89.8% and the 68.5–78.0% to the total seed bank density, respectively. Only a few other species (*Gypsophila muralis, Lythrum hyssopifolia, Spergularia salina* and *Trifolium angulatum*) possessed higher seed densities than 1000 seeds/m^2 in this type of grasslands. Several species like *Centaurium minus*, *C. pulchellum* and *Medicago lupulina* had no germinated seeds in the two types of *Puccinellia* grasslands, only in the *Artemisia* and *Juncus* grasslands (Table A2). The majority of hygrophyte species possessed highest seed densities in *Juncus* grasslands (like *Agrostis stolonifera*, *Bolboschoenus maritimus* and *Lythrum hyssopifolia*) or in *Juncus* and *Artemisia* grasslands (like *Centaurium minus* and *C. pulchellum*) or in *Artemisia* grasslands (*Typha* spp.; Fig. 1, Table A2). We found that all of the most frequent seed bank species had germinated seeds in *Juncus* grasslands (Table A2).

4. Discussion

4.1. Similarity of vegetation and seed banks

We detected more species in the seed bank than in the aboveground vegetation which emphasises that seed bank plays an important role in sustaining the diversity of alkali grasslands. The similarity of vegetation and seed bank was low in every studied grassland types (for detailed species composition see Table A3). Sørensen similarity scores ranged from 0.37 in *Puccinellia* high grasslands to 0.47 in *Juncus* grasslands (see Table 2). These mean scores are lower than the mean similarity scores (0.54) found for grasslands, but somewhat higher than mean scores found for wetlands (0.40) in the review of Hopfensperger (2007). The low similarity scores detected in our study might be caused by (i) the lack of persistent seed bank of characteristic grass species and (ii)

Table 2
Vegetation and seed bank characteristics and Sørensen similarity of vegetation and seed bank of grasslands (mean ± SD). Significant differences between studied grassland types are indicated using different superscripted letters (one-way ANOVA and Tukey test). n.s.: non significant. *Species numbers in seed bank are given for 3 cores from the same plot (37.68 cm^2); for grassland codes (see Table 1).

	$F_{3,12}$	p	AG	PHG	PLG	JG
Vegetation						
Species number						
Total	0.939	n.s.	10.5 ± 0.8	8.7 ± 4.0	11.7 ± 2.4	11.5 ± 1.5
Hygrophytes	13.595	**	1.7 ± 0.3[a]	1.6 ± 0.3[a]	2.5 ± 0.5[a]	3.6 ± 0.5[b]
Halophytes	91.986	***	2.1 ± 0.1[a]	4.5 ± 0.3[b]	5.0 ± 0.2[b]	2.2 ± 0.4[a]
Cover (%)						
Hygrophytes	5.517	*	6.4 ± 6.6[a]	41.3 ± 26.9[ab]	27.7 ± 3.8[ab]	50.3 ± 3.7[b]
Halophytes	87.746	***	6.5 ± 0.3[a]	84.9 ± 12.1[c]	72.8 ± 0.3[c]	38.7 ± 5.0[b]
Shannon diversity	2.322	n.s.	1.1 ± 0.2	1.3 ± 0.4	1.6 ± 0.2	1.3 ± 0.5
Seed bank						
Species number*						
Total	3.077	n.s.	7.7 ± 0.6	4.8 ± 0.9	6.9 ± 2.8	10.1 ± 3.0
Hygrophytes	3.274	n.s.	2.4 ± 0.5	1.7 ± 0.1	3.0 ± 1.8	4.9 ± 1.8
Halophytes	0.890	n.s.	1.1 ± 0.2	1.9 ± 0.3	1.5 ± 0.9	1.5 ± 0.4
Seed density (seeds/m^2)						
Total	0.749	n.s.	36,287 ± 19,550	30,104 ± 13,081	34,591 ± 17,826	51,410 ± 22,343
Hygrophytes	2.053	n.s.	28,938 ± 21,245	5123 ± 3216	21,359 ± 26,024	46,022 ± 23,381
Halophytes	4.623	*	1343 ± 391[a]	23,709 ± 11,655[b]	11,678 ± 11,527[ab]	2880 ± 2081[ab]
Juncus spp.	1.862	n.s.	28,231 ± 21,076	4894 ± 3155	19,221 ± 23,073	38,619 ± 18,182
Shannon diversity*	0.798	n.s.	1.0 ± 0.4	0.7 ± 0.1	0.8 ± 0.2	1.0 ± 0.2
Sørensen similarity	1.439	n.s.	0.46 ± 0.08	0.37 ± 0.02	0.46 ± 0.08	0.47 ± 0.04

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

also because several hygrophytes present in the seed bank are absent from the vegetation of the studied grassland types.

4.2. Salinity, stress and seed banks

Among salt-affected habitats, alkali grasslands are characterised by low to medium salinity scores (0.98 up to 2.80 mS/cm in his study; 0.1–3.2 mS/cm in Szabó and Tóth, 2011). In other types of saline grasslands and salt marshes higher scores were reported (up to 58.6 mS/cm, Anatolian saline grasslands, Gokalp et al., 2010; 2.0–64.0 mS/cm, inland saline meadows, Piernik, 2003). For salt marshes and salt deserts also generally high scores were detected (for coastal salt marshes 4.0–8.3 mS/cm, Kilinc et al., 2011; Maranón, 1998; for inland salt marshes: 3.5–16.0 mS/cm; Neill, 1993; 55–191 mS/cm in salt deserts of Pakistan, Zia et al., 2007). Higher salinity in salt marshes compared to the studied alkali grasslands can also explain the differences in seed density as high levels of salinity can preserve high amount of seeds of salt-tolerant halophyte species (Adam, 1990). In our study, *Spergularia salina* had the highest seed density (mean density of 23,108 seeds/m^2) among halophytes, even it was present with low cover scores (mean scores lower than 5%) in *Puccinellia* high grasslands.

The detected mean seed bank density scores ranging from 30,104 to 51,410 seeds/m^2 are higher than was found in most dry grasslands (e.g. in calcareous grasslands, about 200–900 seeds/m^2; Bossuyt et al., 2006; Kalamees and Zobel, 1998), but fall in the lower part of the seed density range detected in grasslands (10^3–10^6 seeds/m^2; Bossuyt and Honnay, 2008; Fenner and Thompson, 2005; Schmiede et al., 2009). Given the fact that no studies on alkali grassland seed bank were published yet, our results can be compared only with studies in salt marshes and seashore meadows. Several studies detected considerably lower seed density scores in coastal (e.g. 27 seeds/m^2, Hutchings and Russell, 1989; 330 seeds/m^2, Crain et al., 2008) or in inland salt marshes (e.g. 850 seeds/m^2, Smith and Kadlec, 1983), and salt deserts (1000–2000 seeds/m^2, Khan, 1993) compared to our findings. In contrast, some of the highest seed bank densities ever reported is from inland salt marshes (e.g. 140,000 seeds/m^2, Jerling, 1983; 479,200 seeds/m^2, Badger and Ungar, 1994). In our study, only a few species possessed dense soil seed bank. Out of the most abundant species of the aboveground vegetation of the four grassland types, *Juncus compressus* group was the only one with dense seed bank (up to a density of 38,619 seeds/m^2). Characteristic grasses like *Festuca pseudovina, Hordeum hystrix* and *Puccinellia limosa* had at most sporadic seed banks (a maximum of 265 seeds/m^2). These results are in line with former findings in seashore meadows and salt marshes, where for the characteristic perennial grasses like *Spartina* spp. no persistent seed bank was found (Hopkins and Parker, 1984; Ungar, 2001).

Validating the empirical stress gradient published by Kelemen et al. (2013), we found that *Juncus* grasslands at the lowest elevations were the least stressed grassland types characterised by the lowest salinity and the highest soil water capacity, soil organic matter and soil water contents. The most stressed grassland types were *Puccinellia* high grasslands at medium elevations with the highest salinity, and the lowest scores for soil water capacity, soil organic matter and soil water contents. The most marked differences between aboveground vegetation and seed bank were found also in the *Puccinellia* high grasslands, where a high aboveground diversity was detected parallel with the lowest seed bank diversity.

It was formerly found that seed bank diversity and density can be very high in stressed grasslands, where regeneration by seeds can play an essential role in plant establishment because of the unfavourable environmental conditions (Hopfensperger, 2007; Bossuyt and Honnay, 2008). Thus, we hypothesised that species diversity and density of the seed bank are the highest in the most stressed grassland types, where regeneration by seeds could have a major importance in sustaining vegetation diversity. Surprisingly, this hypothesis was not supported by our results, as we detected both the lowest seed bank density and diversity in *Puccinellia* high grasslands. In *Puccinellia* high grasslands, *Spergularia salina* was the only abundant seed bank species (possessing at least 1000 seeds/m^2). *Spergularia* species are known to produce very dense persistent seed bank. For *S. marina* the detected seed densities ranging from 350,000 up to a maximum of 1,000,000 seeds/m^2 in the soil of sites, densely covered by the species (Ungar, 1991). We found that out of the frequent seed bank species (listed in Table A2), altogether 11 species present in the seed bank of other grassland

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types were missing from the seed bank of *Puccinellia* high grasslands. A likely explanation for this phenomenon is that seeds of many glycophyte species perish or are unable to maintain dormancy and/or viability under saline conditions (Ungar, 1991; Ungar and Woodell, 1993). The salt-tolerance of a species can be different in different life-stages; it was found that several halophytes tolerating high salt concentrations as adult plants are sensitive for saline conditions as seeds (Ungar, 2001). Experimental evidence is still missing for the characteristic species detected in alkali grasslands concerning the germination requirements and on the proportion of un-germinated seeds under different salinity conditions. This underlines the necessity of further fine-tuned studies concerning the seed survival, germination and seedling establishment strategy of respective halophytes.

4.3. The seed bank of hygrophytes

We hypothesised that seed density of hygrophytes increases with decreasing elevation, which was partly supported by the results. At the lowest-elevated *Juncus* grasslands we detected the highest seed densities of almost all hygrophyte species. All of the detected hygrophytes possessed viable seeds in this grassland type. Although, we did not find a significant monotonous correlation between elevation and the overall hygrophyte seed bank density; because most of the hygrophyte species were missing from the seed bank at the medium-elevated, but most saline *Puccinellia* grasslands. We detected considerable seed densities of hygrophytes even in the highest-elevated *Artemisia* grasslands (e.g. *Typha* spp.). This fact can be explained by the effective, mainly anemo- or hydrochorous dispersal of hygrophytes which makes them able to accumulate high amounts of seeds even in dry conditions (e.g. in dry sand grasslands, Török et al., 2009).

Among the hygrophytes, *Juncus compressus* group had the highest seed bank density ranging from 4894 up to a density of 38,619 seeds/m^2. *Juncus* species are known to produce high amounts of long-term persistent seeds which can be found in the soil of almost every type of grasslands, marsh communities and even in forests (Bossuyt and Honnay, 2008). Several studies reported that *Juncus* seeds were present in the soil of grasslands where they were at most sporadically present in aboveground vegetation (e.g. in mountain hay meadows, *Juncus conglomeratus* and *J. effusus*, 49,100–76,800 seeds/m^2, Valkó et al., 2011; *J. articulatus, J. bufonius, J. effusus* and *inflexus*, 32–177 seeds/m^2, Reiné et al., 2004). In our study, *Juncus* seeds were found in the soil of every plot in the studied grassland types, but they were detected in high densities especially in *Artemisia* and *Juncus* grasslands. Their density was lower in *Puccinellia* grasslands likely because of the high level of salinity detected there.

4.4. The possible role of persistent seed bank in rapid vegetation changes

We found that seed bank of different grassland types were clearly separated in accordance with the differences in crucial environmental parameters as shown by the CCA (Fig. 1). In contrast to our findings, Ungar and Riehl (1980) found in inland salt marshes that characteristic species of the different vegetation types were present in the seed bank throughout the marsh. They concluded that the seed bank likely represents the regional species pool of the whole habitat complex and enables the shift of vegetation zonation in rapidly changing environments. These findings were not supported by our results. In the present study it was found that only *Juncus compressus* group possessed a dense seed bank in each of the grassland types of the habitat complex. Thus, in alkali grasslands such vegetation zonation shifts like in Ungar and Riehl (1980) are not driven by the local persistent seed bank but more likely by clonal growth and/or spatial seed dispersal.

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Table A1
Cover scores of the characteristic species in the aboveground vegetation of the different grasslands types (mean ± SD). Species with total cover scores of at least 10% are listed. Notations: AG = *Artemisia* grasslands; PHG = *Puccinellia* high grasslands; PLG = *Puccinellia* low grasslands; JG = *Juncus* grasslands.

Species/grassland types	AG	PHG	PLG	JG
Most abundant in AG				
Artemisia santonicum	7.9 ± 8.2	2.3 ± 2.9	1.1 ± 1.4	0.6 ± 1.2
Cynodon dactylon	3.1 ± 7.7			
Festuca pseudovina	59.8 ± 15.1	2.6 ± 4.9	0.6 ± 0.8	1.7 ± 2.4
Podospermum canum	0.9 ± 0.5	0.1 ± 0.1		
Trifolium retusum	1.5 ± 1.6	0.8 ± 2.0	0.5 ± 0.9	0.1 ± 0.2
Most abundant in AG and JG				
Carex stenophylla	2.7 ± 2.8		0.6 ± 2.1	3.9 ± 4.1
Trifolium fragiferum	0.7 ± 2.6			0.5 ± 1.5
Most abundant in JG				
Agrostis stolonifera		0.1 ± 0.1	0.2 ± 0.3	1.6 ± 3.5
Bupleurum tenuissimum	0.3 ± 0.4	0.1 ± 0.1	0.2 ± 0.4	0.7 ± 1.0
Hordeum hystrix	5.0 ± 5.9	15.1 ± 15.3	25.3 ± 12.2	34.9 ± 8.7
Inula britannica	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.6 ± 1.4
Juncus compressus	4.8 ± 6.6	0.3 ± 1.0	5.2 ± 9.2	43.2 ± 11.7
Trifolium angulatum	0.8 ± 1.2	0.5 ± 1.1	1.0 ± 1.5	2.1 ± 1.7
Most abundant in PHG				
Puccinellia limosa	0.1 ± 0.3	18.4 ± 12.8	12.1 ± 9.6	1.9 ± 2.2
Spergularia media	0.4 ± 0.6	0.7 ± 1.0	0.5 ± 0.5	0.1 ± 0.1
Spergularia salina	0.1 ± 0.2	4.9 ± 8.8	1.3 ± 2.7	
Most abundant in PLG				
Lepidium ruderale		1.2 ± 1.5	4.8 ± 6.0	
Lotus corniculatus	0.7 ± 0.9	0.9 ± 1.8	1.7 ± 1.8	1.4 ± 1.3
Matricaria chamomilla		2.8 ± 3.6	4.0 ± 4.3	0.1 ± 0.1
Plantago tenuiflora	0.1 ± 0.1	0.9 ± 2.1	1.0 ± 0.9	0.1 ± 0.1
Polygonum aviculare	0.1 ± 0.1	0.2 ± 0.3	0.8 ± 0.9	0.3 ± 0.5

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Table A2
Mean seedling numbers per plot of the characteristic species in the seed bank of the different grasslands types (mean ± SD). Species with total seed densities of at least 3 germinated seedlings are listed. For grassland codes see Table A1. One geminated seedling corresponds with a seed density of 265 seeds/m^2.

Species/grassland types	AG	PHG	PLG	JG
Most abundant in AG				
Festuca pseudovina	1.0 ± 1.1	0.7 ± 1.0	0.8 ± 1.4	0.1 ± 0.5
Trifolium angulatum	14.9 ± 11.5	1.0 ± 1.6	3.9 ± 8.7	4.4 ± 7.7
Trifolium retusum	2.6 ± 5.1			0.1 ± 0.5
Typha spp.	0.3 ± 0.6	0.2 ± 0.4	0.1 ± 0.4	0.1 ± 0.4
Most abundant in AG and JG				
Carex stenophylla	1.7 ± 1.7	0.6 ± 2.1	0.3 ± 0.5	1.5 ± 2.0
Centaurium minus	1.0 ± 1.7		0.1 ± 0.3	0.7 ± 1.1
Centaurium pulchellum	1.2 ± 2.5		0.1 ± 0.3	2.5 ± 6.3
Juncus compressus	106.5 ± 99.1	18.5 ± 22.6	72.5 ± 79.3	145.7 ± 81.4
Medicago lupulina	0.1 ± 0.4			0.2 ± 0.6
Polygonum aviculare	0.5 ± 0.7	0.2 ± 0.4	0.1 ± 0.4	0.7 ± 1.0
Most abundant in JG				
Agrostis stolonifera	0.1 ± 0.3			0.6 ± 1.8
Bolboschoenus maritimus			0.1 ± 0.5	0.3 ± 0.8
Bupleurum tenuissimum	0.1 ± 0.4	0.1 ± 0.3	0.6 ± 1.1	3.2 ± 6.6
Gypsophila muralis	0.8 ± 1.1	0.1 ± 0.4	1.2 ± 1.9	4.5 ± 4.4
Inula britannica			1.0 ± 1.6	1.4 ± 1.8
Lotus corniculatus	0.3 ± 0.8		0.3 ± 0.5	0.9 ± 0.8
Lythrum hyssopifolia			4.3 ± 9.7	13.7 ± 14.8
Plantago major				0.3 ± 1.0
Rorippa kerneri		0.3 ± 0.8		1.3 ± 3.4
Most abundant in PHG				
Camphorosma annua		0.9 ± 2.6	0.3 ± 1.0	0.1 ± 0.3
Myosotis stricta		2.3 ± 9.0		0.1 ± 0.3
Spergularia salina	4.6 ± 4.4	87.2 ± 80.9	41.2 ± 52.7	9.6 ± 10.7
Most abundant in PLG				
Matricaria chamomilla	0.3 ± 0.8	1.1 ± 1.4	2.3 ± 3.9	1.0 ± 1.6
Mentha pulegium			0.5 ± 1.8	0.1 ± 0.5

Table A3
Cover scores and seedling numbers per plot of the characteristic species present only in the vegetation, both in the vegetation and seed bank and only in the seed bank of the different grasslands types (mean ± SD). Species with total cover scores of at least 10% or total seed densities of at least 3 germinated seedlings are listed. For grassland codes see Table A1. One geminated seedling corresponds with a seed density of 265 seeds/m^2.

	Vegetation				Seed bank			
	AF	PH	PL	JU	AF	PH	PL	JU
Species present only in the vegetation								
Cynodon dactylon	3.1 ± 7.7							
Lepidium ruderale		1.2 ± 1.5	4.8 ± 6.0					
Podospermum canum	0.9 ± 0.5	0.1 ± 0.1						
Species present in the vegetation and seed bank								
Agrostis stolonifera		0.1 ± 0.1	0.2 ± 0.3	1.6 ± 3.5	0.1 ± 0.3			0.6 ± 1.8
Artemisia santonicum	7.9 ± 8.2	2.3 ± 2.9	1.1 ± 1.4	0.6 ± 1.2			0.1 ± 0.5	
Aster tripolium	0,07	0,05		0,10			0.1 ± 0.5	0.1 ± 0.3
Bupleurum tenuissimum	0.3 ± 0.4	0.1 ± 0.1	0.2 ± 0.4	0.7 ± 1.0	0.1 ± 0.4	0.1 ± 0.3	0.6 ± 1.1	3.2 ± 6.6
Carex stenophylla	2.7 ± 2.8		0.6 ± 2.1	3.9 ± 4.1	1.7 ± 1.7	0.6 ± 2.1	0.3 ± 0.5	1.5 ± 2.0
Festuca pseudovina	59.8 ± 15.1	2.6 ± 4.9	0.6 ± 0.8	1.7 ± 2.4	1.0 ± 1.1	0.7 ± 1.0	0.8 ± 1.4	0.1 ± 0.5
Hordeum hystrix	5.0 ± 5.9	15.1 ± 15.3	25.3 ± 12.2	34.9 ± 8.7		0.1 ± 0.3		
Inula britannica	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.6 ± 1.4			1.0 ± 1.6	1.4 ± 1.8
Juncus compressus	4.8 ± 6.6	0.3 ± 1.0	5.2 ± 9.2	43.2 ± 11.7	106.5 ± 99.1	18.5 ± 22.6	72.5 ± 79.3	145.7 ± 81.4
Lotus corniculatus	0.7 ± 0.9	0.9 ± 1.8	1.7 ± 1.8	1.4 ± 1.3	0.3 ± 0.8		0.3 ± 0.5	0.9 ± 0.8
Matricaria chamomilla		2.8 ± 3.6	4.0 ± 4.3	0.1 ± 0.1	0.3 ± 0.8	1.1 ± 1.4	2.3 ± 3.9	1.0 ± 1.6
Mentha pulegium				0.1 ± 0.3			0.5 ± 1.8	0.1 ± 0.5
Plantago tenuiflora	0.1 ± 0.1	0.9 ± 2.1	1.0 ± 0.9	0.1 ± 0.1			0.1 ± 0.3	
Poa angustifolia			0.1 ± 0.1	0.5 ± 1.6	0.1 ± 0.3	0.1 ± 0.5	0.1 ± 0.3	
Polygonum aviculare	0.1 ± 0.1	0.2 ± 0.3	0.8 ± 0.9	0.3 ± 0.5	0.5 ± 0.7	0.2 ± 0.4	0.1 ± 0.4	0.7 ± 1.0
Puccinellia limosa	0.1 ± 0.3	18.4 ± 12.8	12.1 ± 9.6	1.9 ± 2.2		0.2 ± 0.6	0.1 ± 0.3	
Spergularia media	0.4 ± 0.6	0.7 ± 1.0	0.5 ± 0.5	0.1 ± 0.1	0.1 ± 0.5			
Spergularia salina	0.1 ± 0.2	4.9 ± 8.8	1.3 ± 2.7		4.6 ± 4.4	87.2 ± 80.9	41.2 ± 52.7	9.6 ± 10.7
Trifolium angulatum	0.8 ± 1.2	0.5 ± 1.1	1.0 ± 1.5	2.1 ± 1.7	14.9 ± 11.5	1.0 ± 1.6	3.9 ± 8.7	4.4 ± 7.7
Trifolium fragiferum	0.7 ± 2.6			0.5 ± 1.5	0.1 ± 0.3			0.1 ± 0.4
Trifolium retusum	1.5 ± 1.6	0.8 ± 2.0	0.5 ± 0.9	0.1 ± 0.2	2.6 ± 5.1			0.1 ± 0.5
Species present only in the seed bank								
Bolboschoenus maritimus							0.1 ± 0.5	0.3 ± 0.8
Camphorosma annua						0.9 ± 2.6	0.3 ± 1.0	0.1 ± 0.3
Centaurium minus					1.0 ± 1.7		0.1 ± 0.3	0.7 ± 1.1
Centaurium pulchellum					1.2 ± 2.5		0.1 ± 0.3	2.5 ± 6.3
Gypsophila muralis					0.8 ± 1.1	0.1 ± 0.4	1.2 ± 1.9	4.5 ± 4.4
Lythrum hyssopifolia							4.3 ± 9.7	13.7 ± 14.8
Medicago lupulina					0.1 ± 0.4			0.2 ± 0.6
Myosotis cf. *stricta*						2.3 ± 9.0		0.1 ± 0.3
Plantago major								0.3 ± 1.0
Plantago maritima							0.1 ± 0.3	0.1 ± 0.4
Rorippa kerneri						0.3 ± 0.8		1.3 ± 3.4
Typha spp.					0.3 ± 0.6	0.2 ± 0.4	0.1 ± 0.4	0.1 ± 0.4

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Appendix A.

See Tables A1–A3.

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