





RESEARCH ARTICLE

Dynamics in vegetation and seed bank composition highlight the importance of post-restoration management in sown grasslands

Orsolya Valkó¹ , Balázs Deák^{1,2} , Péter Török^{3,4} , Katalin Tóth³, Réka Kiss¹, András Kelemen¹, Tamás Migléc³, Judit Sonkoly⁴, Béla Tóthmérész⁵ 

Sowing grasses supports the rapid development of a closed perennial vegetation, which makes the method universally suitable for fast and effective landscape-scale restoration of grasslands. However, to increase their diversity and to create a natural-like species-rich grassland is a challenging task. Understanding the role of seed bank compositional changes and vegetation dynamics can help to design management regimes that support the establishment of target species and suppress unwanted weeds. Our aim was to reveal the effect of post-restoration management on the vegetation and seed bank dynamics in grasslands restored in one of the largest European landscape-scale restoration projects. Eight years after restoration, we sampled the vegetation and the seed bank in 96 quadrats located in 12 restored grasslands in the Great Hungarian Plain. In each grassland stand, we studied and compared a mown (mown from Year 1 to Year 8) and an abandoned plot (mown from Year 1 to Year 3 then abandoned from Year 4 to Year 8). Mown and abandoned plots showed divergent vegetation and seed bank development. Abandonment led to the decline of sown grasses and higher cover of weeds, especially in the alkaline grasslands. Our study underlined that the developing seed bank had a limited contribution to the maintenance of biodiversity in both grassland types. We found that 5 years of abandonment had a larger effect on the seed bank than on the vegetation. We stress that long-term management is crucial for controlling the emergence of the weeds from their dense seed bank in restored grasslands.

Key words: abandonment, alkaline grassland, cessation of mowing, grassland restoration, loess grassland, seed bank, seed sowing, weed encroachment

Implications for Practice

- Seed sowing of grass mixtures is a feasible tool for restoring grasslands at large scales. However, the resulting vegetation usually has low biodiversity, and a high density of weed seeds is accumulating in the soil seed bank even several years after the restoration. Therefore, post-restoration management is necessary for suppressing weeds both above- and belowground.
- We recommend designing the long-term management of grassland restoration sites already when planning the restoration projects to ensure the management plan is ecologically and economically feasible.
- We recommend complementing the monitoring of vegetation development with the analysis of soil seed banks for evaluating long-term restoration success.

Introduction

The restoration of degraded ecosystems is an important strategy to mitigate the negative impacts of human activities on Earth. Grassland restoration is widely applied in nature conservation to increase landscape connectivity, create habitats for plants and animals, and restore important ecosystem functions and services (Cole et al. 2019). Best practices for the fast and successful

restoration of grasslands with high cover of perennial grasses and low cover of unwanted weeds are well established and widely applied (Kiehl et al. 2010; Török et al. 2011).

In many cases, introduction of seeds to restoration sites is crucial for guaranteeing restoration success and ensuring colonization by target species which are locally absent. Seed sowing is especially recommended in large restoration sites in human-

Author contributions: BT, PT, BD, OV designed the experiment; OV, BD, PT, KT, RK, AK, TM, SJ collected the data; BD, OV analyzed the data; OV wrote the manuscript and all authors contributed critically to the drafts and gave final approval for publication.

¹MTA-ÖK Lendület Seed Ecology Research Group, Institute of Ecology and Botany, Centre for Ecological Research, Alkotmány út 2-4, 2163, Vácrátót, Hungary

²Address correspondence to B. Deák, email debalazs@gmail.com

³Department of Ecology, Faculty of Science and Technology, University of Debrecen, Egyetem sqr. 1, 4032, Debrecen, Hungary

⁴MTA-DE Lendület Functional and Restoration Ecology Research Group, Egyetem sqr. 1, 4032, Debrecen, Hungary

⁵MTA-DE Biodiversity and Ecosystem Services Research Group, Egyetem sqr. 1, 4032, Debrecen, Hungary

© 2020 The Authors. Restoration Ecology published by Wiley Periodicals, Inc. on behalf of Society for Ecological Restoration.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

doi: 10.1111/rec.13192

Supporting information at:

<http://onlinelibrary.wiley.com/doi/10.1111/rec.13192/supinfo>

modified landscapes and in areas subjected to long-lasting or severe degradation, where restoration potential of the seed bank is limited (Török et al. 2018). Dry grasslands in general have a low-density seed bank, characterized by a dominance of transient seeds, and containing just a few persistent seeds of only few typical, rare, or endangered grassland species (Bossuyt & Honnay 2008; Kiss et al. 2016; Godefroid et al. 2018). Therefore, sowing seeds of rare target species is a widely applied species introduction method in dry grassland restoration projects (Barr et al. 2017). However, the availability of seed material of regional provenance is often a major limiting factor in restoration projects (de Vitis et al. 2017), and especially in large-scale projects only a limited number of target species can be included in the seed mixtures (Kiss et al. 2020).

Sowing a grass-dominated seed mixture guarantees a directed vegetation development and a cost-effective way of restoration (Kiehl et al. 2010; Török et al. 2011). In such projects, the most challenging task is to select the right species of local provenance and to choose a proper seed density (van der Mijnsbrugge et al. 2010; de Vitis et al. 2017). After sowing the seed mixture, a fast and successful grassland recovery can be expected (Baer et al. 2002; Török et al. 2010; Deal et al. 2014). Even though the initial vegetation is usually characterized by weeds emerging from the seed bank of the formerly degraded areas, sown grasses can competitively exclude such (annual or biennial) species from the aboveground vegetation after 2 or 3 years (Török et al. 2010). Therefore, if good seed material and well-suited machinery are provided, seed sowing can be a feasible tool for restoring basic grassland vegetation on large spatial scales. In the United States, grassland restoration by seed sowing on former croplands covers millions of hectares (Baer et al. 2002), while in Europe, seed-sowing projects can reach the extent of several hundreds of hectares (Török et al. 2010).

The long-term maintenance of restored grasslands is a challenging task. First, low-diversity communities are often more sensitive to disturbances because they are less stable than high-diversity communities (Oliver et al. 2015). Greater species richness promotes stability, because there are high numbers of species that respond differently to the environmental fluctuations, so the decline of one of them could be compensated by the strengthening of another one (Lepš 2004). Second, the legacy of the former degradation or disturbance, especially in the form of the seed bank of weeds, acts as a threat for future development in the species-poor restored grasslands (Halassy 2001; Walker et al. 2004; Török et al. 2012). Finally, a dense grass sward hampers the establishment of target grassland species, but if the grassland is disturbed, there is a higher chance for weeds to establish, due to their increased propagule availability (Klaus et al. 2018). Considering these risks and threats, it is crucial to develop long-term management strategies to avoid degradation of the newly restored grasslands (Kelemen et al. 2014). Regular mowing or grazing is essential to prevent weed encroachment and litter accumulation, and to create establishment microsites for target species (Tälle et al. 2016).

In this study, we tested the effects of post-restoration management (mowing vs. abandonment) on the vegetation and seed bank of alkaline and loess grasslands, which were restored

during one of the largest grassland restoration projects in Europe, where seeds of native grasses, primarily from local provenance, were sown (LIFE 04 NAT HU 119, “Grassland restoration and marsh protection in Egyek-Pusztakócs” LIFE project). Alkaline grasslands are typical on nutrient-poor, saline soils, and usually have a species-poor vegetation (Deák et al. 2014), but a diverse and dense seed bank (Valkó et al. 2014). Loess grasslands are typical on fertile chernozem soils and are characterized by high plant diversity in the aboveground vegetation (Kelemen et al. 2013), and low seed density and diversity in the seed bank (Tóth & Hüse 2014). This study system offers a unique opportunity for testing the effects of post-restoration management on the vegetation and seed bank of two different types of restored grasslands.

We tested the following hypotheses: (1) Abandoned restored grasslands are characterized by lower species richness, lower cover of sown native perennial grasses, and higher cover of unwanted weeds compared to mown ones (Kelemen et al. 2014). (2) The effects of abandonment depend on grassland type and we expect that, due to their poor seed bank (Tóth & Hüse 2014), restored loess grasslands are more sensitive to abandonment than restored alkaline grasslands (Valkó et al. 2014). (3) The effect of abandonment is more pronounced in the aboveground vegetation of the restored grasslands compared to the seed bank as vegetation changes faster than seed bank (Miao et al. 2016).

Methods

Study Area

Our study area is in the Hortobágy National Park (Great Hungarian Plain), near Tiszafüred and Egyek towns. The climate of the region is moderately continental with a mean annual precipitation of 550 mm and a mean temperature of 9.5°C (Lukács et al. 2015). The National Park holds one of the largest remaining natural open landscapes in Europe, characterized by a diverse mosaic of loess and alkaline grasslands, meadows, and wetlands (Deák et al. 2014). Because of their fertile chernozemic soils, many stands of loess grasslands have been converted to arable fields, and in some regions, large stands of alkaline grasslands with less fertile meadow solonetz soil were also plowed. The most typical crop plants in the region are alfalfa (*Medicago sativa*), sunflower (*Helianthus annuus*), and wheat (*Triticum aestivum*) (Török et al. 2012).

Restoration Project

In the study area, in total 760 ha of grasslands were restored on former croplands, which was one of the largest grassland restoration projects in Europe (LIFE 04 NAT HU 119). The aim of the landscape-scale restoration project was to create buffer zones around wetlands and to restore the historical landscape connectivity (Lengyel et al. 2012). The two target habitats were alkaline grasslands (Natura 2000 habitat *1530: Pannonic salt steppes and salt marshes, habitat of special community interest; ŠeffEROVÁ StanOVÁ et al. 2008) and loess grasslands (Natura 2000 habitat 6250: Pannonic loess steppic grassland, habitat of

community interest; European Commission 2013). Two types of grass seed mixtures were sown after soil preparation in a density of 25 kg/ha in October 2005 (Deák et al. 2011). To restore alkaline grasslands, on lower-elevated (<90 m a.s.l.) sites an “alkaline seed mixture” containing the seeds of *Festuca pseudovina* (66%) and *Poa angustifolia* (34%) was sown. To restore loess grasslands, on higher-elevated (>90 m a.s.l.) sites the sown “loess seed mixture” contained the seeds of *F. rupicola* (40%), *P. angustifolia* (30%), and *Bromus inermis* (30%) (Török et al. 2010). These perennial grass species were selected because they are typical in the region, their seeds were available from regional provenance, and they are good competitors that can suppress weeds. The seeds used for restoration were from local provenance: *Festuca* seeds were harvested in the grasslands in the region, while seeds of *P. angustifolia* and *B. inermis* were purchased from a company, but the seed stock originated from the study region.

Vegetation Sampling

We selected 12 restored grasslands for the study (mean \pm SD size of restored grasslands is 25.5 ± 14.7 ha), seven of them were alkaline and five were loess grasslands. We designated two 5 m \times 5 m-sized plots in each grassland. One of the plots was “mown” and has been mown every year by hand in the middle of June, from Year 1 to Year 8. The other plot was “abandoned” and was only mown between Year 1 and Year 3, but mowing was stopped from Year 4 onwards. This way we tested the effects of abandonment of post-restoration management on the vegetation and seed banks of restored grasslands. In each 5 m \times 5 m-sized plot we designated four 1 m \times 1 m-sized permanent quadrats, where we recorded vegetation data and sampled soil seed banks. For this study, we used data from Year 8 (2013). During the vegetation survey, percentage cover of vascular plants was recorded in early June in the 1 m \times 1 m quadrats. Nomenclature follows Király (2009).

Seed Bank Sampling

The soil seed bank was sampled in each quadrat in Year 8 in late March, after snowmelt. Three soil cores (4 cm diameter, 10 cm depth) were taken per quadrat. The three cores originating from the same quadrat were pooled and processed together. We concentrated seed bank samples according to the protocol of ter Heerdt et al. (1996) by washing out fine mineral and organic particles to reduce sample volume. Larger plant particles were retained with a coarse mesh (2.8 mm) and were disposed, while seeds were retained using a fine mesh (0.2 mm). Concentrated samples were spread in a thin layer on the surface of steam-sterilized potting soil in germination boxes (15 cm \times 60 cm). Samples were germinated under natural light conditions in an unheated greenhouse from early April until early November. Samples were watered regularly, but from mid-July to mid-August we included a drought period when we did not water the pots in order to mimic natural summer drought conditions typical in the studied grasslands. Germinated seedlings were regularly counted and identified, while unidentifiable seedlings

were transplanted and grown until they developed diagnostic features. Accidental air-borne seed contamination was monitored in control trays filled with steam-sterilized potting soil only.

Data Processing

We pooled *Typha latifolia* and *T. angustifolia* as *Typha angustifolia* (in total 193 seedlings) in the analyses as we could not distinguish the germinated specimens due to the lack of flowering. We considered adventive species (e.g. *Conyza canadensis*), ruderal competitors (e.g. *Cirsium arvense*), and weed species (e.g. *Descurainia sophia*) as weeds based on the social behavior type classification system of Borhidi (1995). We considered unsown species typical to alkaline and loess grassland habitats as unsown target species (Borhidi 1995). Sown grasses were analyzed separately from naturally established unsown target species. We calculated the Jaccard similarity of the species composition of the vegetation and seed bank for each quadrat.

Effects of “management” (mown, abandoned), “grassland type” (alkaline, loess), and the interaction of “management” and “grassland type” on vegetation and seed bank characteristics were analyzed by generalized linear mixed Models (GLMM) in SPSS 20.0 (Zuur et al. 2009). Grassland stand was included as random factor. Dependent variables for the vegetation were total species richness, and the cover of weeds, sown grasses, and unsown target species. For the seed bank, we included total species richness, and the seed bank density of weeds, sown grasses, and unsown target species. In the case of seed density of target species, substantial zero-inflation was observed; therefore, we fitted a Poisson GLMM with control for zero-inflation, using automatic differentiation model building GLMM of the R-package “glmmADMB” (Fournier et al. 2012; Skaug et al. 2016). We identified indicator species of the vegetation and seed bank with the IndVal procedure (Dufrêne & Legendre 1997), using the “labdsv” package in an R environment (R Core Team 2016). Species composition of the vegetation and seed bank was visualized by DCA (detrended correspondence analysis) ordination, based on relative abundance data of species using CANOCO 5 (ter Braak & Šmilauer 2012).

Results

We found in total 165 species in the studied grasslands. One hundred and six species were recorded in the aboveground vegetation and 129 in the seed bank. Of these, 36 species were present in the vegetation only, 59 in the seed bank only, and 70 both in vegetation and seed bank. The Jaccard similarity of the species composition of the vegetation and seed bank was low (0.16 ± 0.07 , mean \pm SD) regardless of management and grassland type (Fig. 2B).

Vegetation Characteristics

Total plant species richness of the aboveground vegetation was not significantly affected by management and grassland type (Table S1, Fig. 1A). The cover of unsown target species was

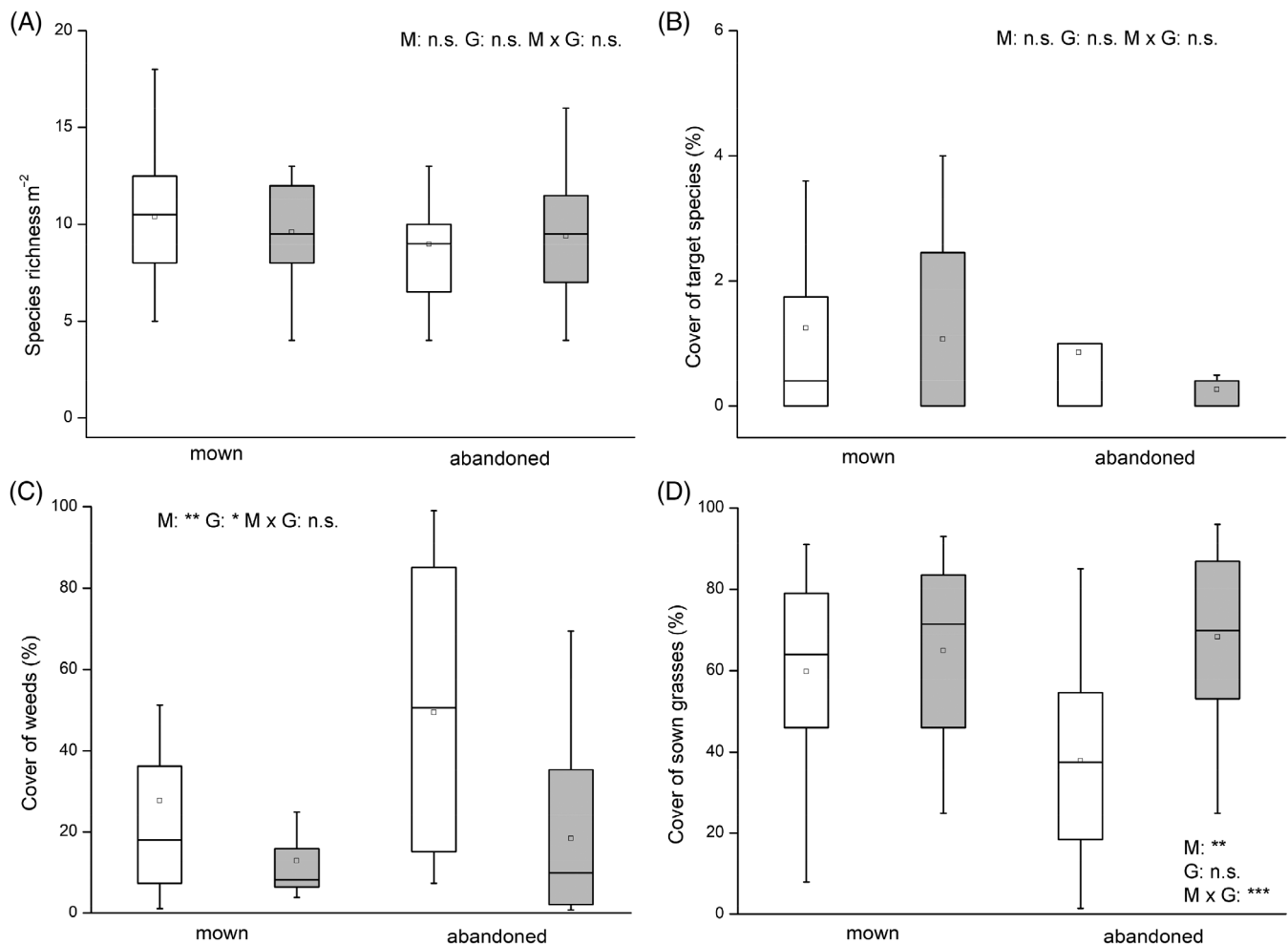


Figure 1. Species richness (A), cover of target species (B), weeds (C), and sown grasses (D) in the vegetation of 8-year-old mown and abandoned restored grasslands. White boxes—Restored alkaline grasslands; gray boxes—Restored loess grasslands. The boxes show the interquartile range, the lower whiskers show the minimum, the upper whiskers show the maximum, and the inner lines display the median values. The results of GLMMs (Table S1) are displayed on each panel using the following notations: M—Effect of management; G—Effect of grassland type; M \times G—Effect of the interaction term between management and grassland type; *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; n.s., not significant.

low, regardless of management and grassland type (Table S1, Fig. 1B). The cover of weeds was affected by management and grassland type (Table S1), with the highest cover of weeds in alkaline grasslands and in abandoned plots (Fig. 1C). The cover of sown grasses was affected by management and the interaction of management and grassland type (Table S1), with highest values in mown plots and lowest cover of sown grasses in abandoned alkaline grasslands (Fig. 1D).

Seed Bank Characteristics

In total 5,045 seedlings germinated from the seed bank samples. Total seed density ranged between 3,183 and 89,127 seeds m^{-2} , mean seed density was 13,939 seeds m^{-2} . Plant species richness of the seed bank was affected by management and grassland type (Table S1). The highest species richness was recorded in mown grasslands (Fig. 2A). Total seed density was affected by

management and the interaction of management and grassland type (Table S1), being highest in mown grasslands and particularly in mown alkaline grasslands (Fig. 2C). Thus, seed density decreased due to abandonment in the loess grasslands (Fig. 2A). Management and the interaction of management and grassland type affected the seed density of weeds (Table S1) showing highest numbers of weed seeds in abandoned alkaline grasslands (Fig. 2D). Both management and grassland type also affected seed density of sown grasses (Table S1) with highest numbers in mown and alkaline grasslands (Fig. 2E). Management type had a significant effect on the seed density of target species (zero-inflated GLMM, $\beta = -1.64$, $z = -5.67$, $p < 0.001$), whereas grassland type did not have a significant effect ($\beta = 0.18$, $z = 0.27$, $p = 0.79$). Also, the interaction term between management and grassland type was significant ($\beta = 1.30$, $z = 3.54$, $p < 0.001$), indicating that management had no significant effect in loess grasslands (Fig. 2F).

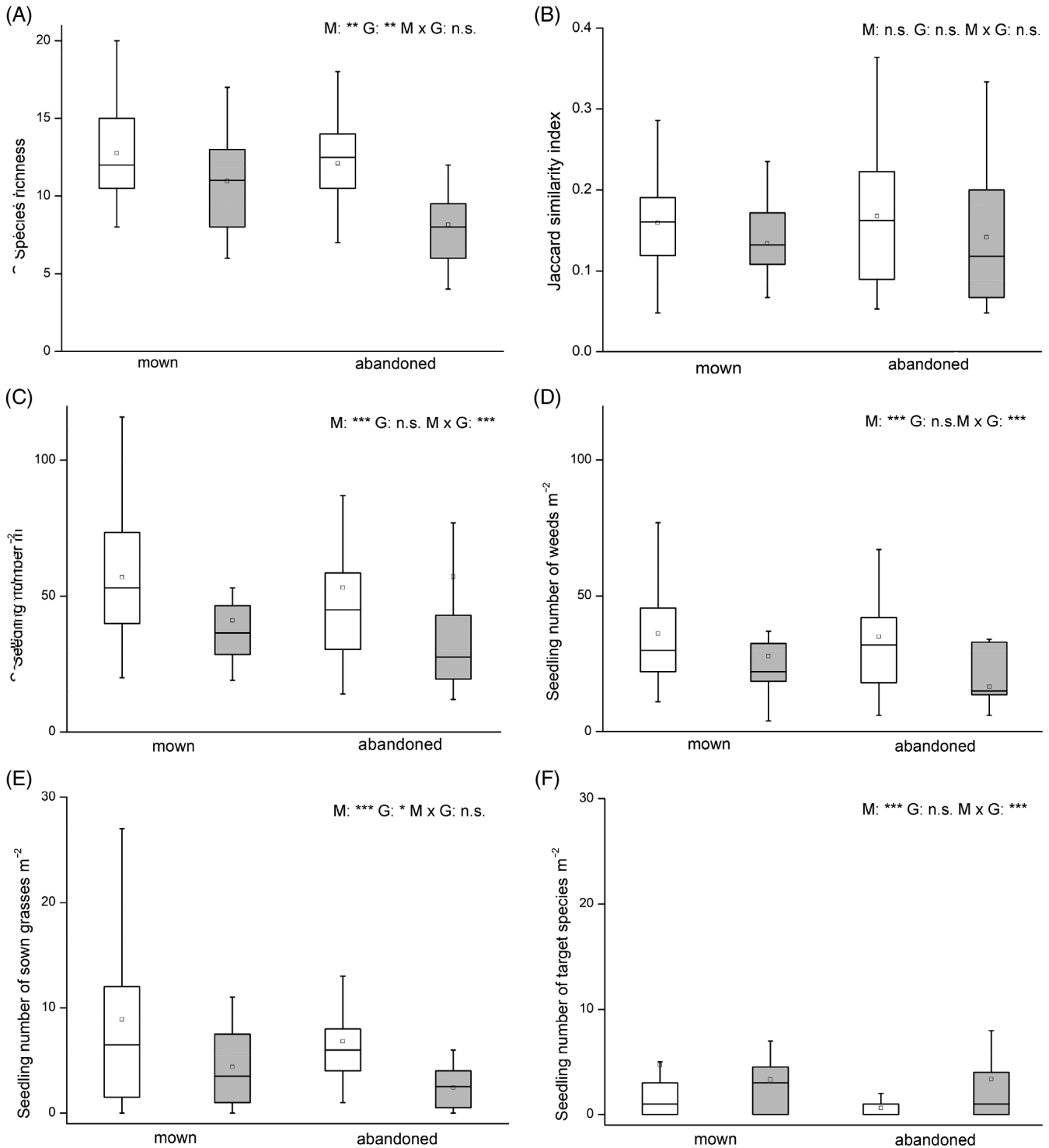


Figure 2. Species richness in the seed bank (A), Jaccard similarity of the vegetation and the seed bank (B), total seed density (C), the seed density of weeds (D), sown grasses (E), and target species (F) in the 8-year-old mown and abandoned restored grasslands. Note that one seedling corresponds to a seed density of 265 seeds m^{-2} . White boxes—Restored alkaline grasslands; gray boxes—Restored loess grasslands. The boxes show the interquartile range, the lower whiskers show the minimum, the upper whiskers show the maximum, and the inner lines display the median values. The results of GLMMs (Table S1) are displayed on each panel using the following notations: M—Effect of management; G—Effect of grassland type; M × G—Effect of the interaction term between management and grassland type; *** $p \leq 0.001$; ** $p \leq 0.01$; * $p \leq 0.05$; n.s., not significant.

Species Composition of the Vegetation and the Seed Bank

In line with the differences in species richness and identity observed (see above), species composition of the vegetation and the seed bank was clearly separated on the DCA ordination (Fig. 3). The seed bank had a generally more homogeneous species composition than the vegetation, shown by a narrow clustering of all seed bank samples. Concerning the vegetation, quadrats sown with alkaline and loess seed mixture were clearly separated, while this was not so obvious for the seed bank. In the vegetation, the species composition of the abandoned quadrats was more heterogeneous compared to the mown ones; in the seed bank, there was no such trend.

Both DCA and Indicator Species analysis confirmed that the initially sown grass species were characteristic for the vegetation of the mown grasslands (*Festuca pseudovina* and *Poa angustifolia* in the alkaline grasslands, and *Bromus inermis* and *F. rupicola* in the loess grasslands; Fig. 3, Table S2). The mown grasslands' vegetation included indicator species for both weeds (*Convolvulus arvensis*, *Vicia villosa*) and target grassland species (*Achillea collina*, *Cruciata pedemontana*, *Trifolium campestre*). There were seven weed species that were characteristic to the vegetation of abandoned grasslands, including *Cirsium arvense*, *Galium spurium*, and *Lactuca serriola*. Characteristic species of the seed bank predominantly included weeds (*Capsella bursa-pastoris*, *Chenopodium album*,

Echinochloa crus-galli) and a few target species (*Inula britannica*, *Matricaria chamomilla*, *Spergularia rubra*; Table S3).

Discussion

Our study confirmed that the cessation of post-restoration management represents a risk for the restored grasslands also in areas where grasslands are less dependent on management than in more temperate regions where forest depicts the climax vegetation. We found that abandoned grasslands are characterized by a lower cover of sown perennial grasses and higher cover of weeds compared to mown ones, which partly confirmed our first hypothesis. We did not detect a decline in species richness in the aboveground vegetation due to abandonment, which is likely due to the generally low species richness of the studied mown and abandoned grasslands. The most abundant weed species of the abandoned grasslands was *Cirsium arvense*, which is among the most troublesome weed species worldwide and the third most noxious weed in Europe (Friedli & Bacher 2001). Its high cover in the vegetation of abandoned grasslands represents a major threat of future encroachment, as the species produces large amounts of long-term persistent seeds, and also effectively spreads vegetatively (Tilley 2010). Balanced against its difficulty as a weed, *C. arvense* is a host to numerous insects, many attracted by copious and accessible nectar and strong flower fragrance (Tilley 2010).

We found that abandoned alkaline and loess grasslands showed distinct vegetation composition: alkaline grasslands were mainly characterized by weeds while loess grasslands were characterized by the high cover of the sown grasses. This partly confirmed our second hypothesis as we found that grassland type affected the vegetation and seed bank of abandoned grasslands. We expected that restored loess grasslands are sensitive to the effects of abandonment, because most target forbs characteristic to loess grasslands do not have persistent seed banks (Tóth & Hüse 2014; Valkó et al. 2014). Even though we detected higher seed densities in alkaline grasslands, the expression of the seed bank was likely hampered by the strong biotic filtering effect of the sown grasses (Deák et al. 2011). In addition, natural loess grasslands are generally sensitive to changes in management (Kelemen et al. 2013). However, in our study, the cover of perennial grasses remained high in abandoned loess grasslands. This can be attributed to the biotic filtering effect of one of the sown grass species, *Bromus inermis*, which is a highly competitive species that could persist in the loess grasslands regardless of abandonment and effectively suppresses weeds in the vegetation (see also Kelemen et al. 2014). However, in the long run, encroachment by *B. inermis* would result in a further decrease in diversity of the loess grasslands.

Our study confirmed the limited potential of the soil seed bank to maintain the species richness of the restored alkaline and loess grasslands. In general, the seed bank was dominated by weeds and there were only a few target species (see also Klaus et al. 2018; Wagner et al. 2018). The similarity of the species composition of vegetation and seed bank was low, as was found in other restored grasslands (Rayburn et al. 2016; Godefroid et al. 2018). Thus, it is likely that abandonment affects

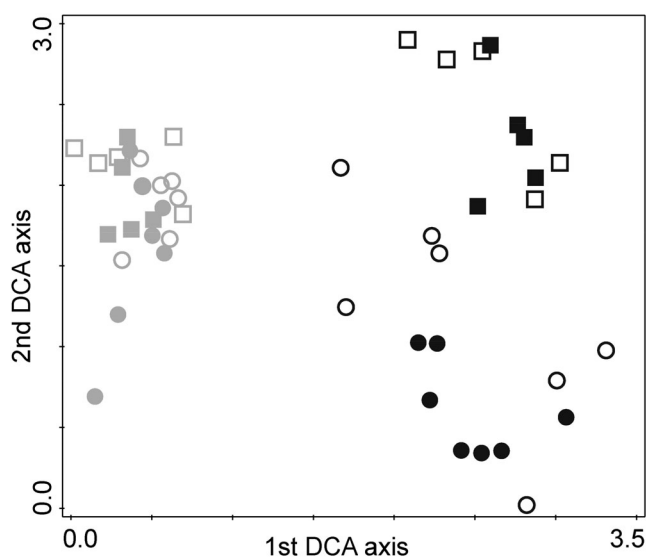


Figure 3. DCA ordination based on the relative abundances of the plant species in the vegetation and seed bank of the restored grasslands. Notations: Black symbols—Vegetation; gray symbols—Seed bank, circles—Alkaline grasslands, squares—Loess grassland; full symbols—Mown sites, empty symbols—Abandoned sites. ●—Vegetation, alkaline grassland, mown; ○—Vegetation, alkaline grassland, abandoned; ■—Vegetation, loess grassland, mown; □—Vegetation, loess grassland, abandoned; ●—Seed bank, alkaline grassland, mown; ○—Seed bank, alkaline grassland, abandoned; ■—Seed bank, loess grassland, mown; □—Seed bank, loess grassland, abandoned. Eigenvalues were 0.565 (first axis) and 0.330 (second axis). Cumulative percentage variance of species data was 9.8% for the first and 15.5% for the second axis, respectively.

the vegetation and seed bank through different mechanisms. Contrary to our third hypothesis, we found that 5 years of abandonment had a larger effect on the seed bank than on the vegetation. Abandonment had a significant effect on all seed bank characteristics. In abandoned grasslands, we found decreased plant species richness and total seed density, increased seed density of weeds, and decreased seed density of sown grasses and target species. In general, the seed bank of the restored grasslands was primarily characterized by annual weeds (more than 70% of all viable seeds), such as *Capsella bursa-pastoris*, *Chenopodium album*, and *Conyza canadensis*. The seed bank of weeds followed the changing vegetation after abandonment (see also Shang et al. 2016). The seed density of weeds increased in the alkaline and decreased in the loess grasslands. The high cover of *B. inermis* in the loess grasslands probably prevented establishment and seed production of weed species and decreased the rate of build-up of their soil seed bank. To the contrary, in abandoned alkaline grasslands, the cover of weeds in the vegetation increased, contributing to the build-up of their seed bank. This was supported by the decreased cover of sown grass species in the abandoned grasslands.

Our findings demonstrate that post-restoration management is important for maintaining the cover of sown grasses and for suppressing weed species, which are still abundant in the vegetation and seed bank. We found that abandonment leads not only to encroachment by weed species in the vegetation, but also to a build-up of their seed bank. When management is stopped a few years after restoration, grasslands become increasingly unattractive for future land use by grazing or mowing due to increasing weed abundance. In regions where animal husbandry is economically profitable, long-term management of the restored meadows and pastures can be ensured (Abson et al. 2017). In other cases, the management of restored grasslands is often guaranteed only in the short term, which is generally limited to the few-years-long maintenance period of the restoration project (Valkó et al. 2018). Our results highlight that it is essential to plan the long-term management of the restored grasslands early in the restoration projects, and to ensure that management is ecologically and economically feasible.

Acknowledgments

The authors are grateful for two anonymous reviewers and to Johannes Kolmann for their comments on the manuscript. We are thankful to the colleagues of Hortobágy National Park Directorate (L. Gál, I. Kapocsi) for their help in fieldwork. Authors were supported by NKFI KH 126476 (OV), NKFI FK 124404 (OV), NKFI KH 130338 (BD), OTKA K 116239 (BT), NKFI KH 126477 (BT), NKFIH K 119225 (PT), NKFI PD 124548 (TM), NKFI PD 128302 (KT), MTA's Post-Doctoral Research Program (AK), and the Bolyai János Fellowship of the Hungarian Academy of Sciences (OV, BD, AK).

Literature Cited

- Abson DJ, Fischer J, Leventon J, Newig J, Schomerus T, Vilsmaier U, et al. (2017) Leverage points for sustainability transformation. *Ambio* 46:30–39
- Baer S, Kitchen D, Blair J, Rice C (2002) Changes in ecosystem function along a chronosequence of restored grasslands. *Ecological Applications* 12: 1688–1701
- Barr S, Jonas JL, Paschke MW (2017) Optimizing seed mixture diversity and seeding rates for grassland restoration. *Restoration Ecology* 25:396–404
- Borhidi A (1995) Social behaviour types, the naturalness and relative indicator values of the higher plants in the Hungarian flora. *Acta Botanica Hungarica* 39:97–181
- Bossuyt B, Honnay O (2008) Can the seed bank be used for ecological restoration? An overview of seed bank characteristics in European communities. *Journal of Vegetation Science* 19:875–884
- ter Braak CJF, Šmilauer P (2012) Canoco reference manual and user's guide: software for ordination, version 5.0. Microcomputer power, Ithaca, New York
- Cole AJ, Griffiths RI, Ward SE, Whitaker J, Ostle NJ, Bardgett RD (2019) Grassland biodiversity restoration increases resistance of carbon fluxes to drought. *Journal of Applied Ecology* 56:1806–1816
- Core Team R (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- De Vitis M, Abbandonato H, Dixon K, Laverack G, Bonomi C, Pedrini S (2017) The European native seed industry: characterization and perspectives in grassland restoration. *Sustainability* 9:1682
- Deák B, Valkó O, Kelemen A, Török P, Miglécz T, Ölvedi T, Lengyel S, Tóthmérész B (2011) Litter and graminoid biomass accumulation suppresses weedy forbs in grassland restoration. *Plant Biosystems* 145: 730–737
- Deák B, Valkó O, Alexander C, Mücke W, Kania A, Tamás J, Heilmeyer H (2014) Fine-scale vertical position as an indicator of vegetation in alkaline grasslands – case study based on remotely sensed data. *Flora* 209:693–697
- Deal M, Xu J, John R, Zenone T, Chen J, Chu H, Jasrotia P, Kahmark K, Bossenbroek J, Mayer C (2014) Net primary production in three bioenergy crop systems following land conversion. *Journal of Plant Ecology* 7:451–460
- Dufréne M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345–366
- European Commission (2013) Pages 146. Interpretation manual for European Union habitats. European Commission DG Environment, Brussels, Belgium
- Fournier DA, Skaug HJ, Ancheta J, Ianelli J, Magnusson A, Maunder MN, Nielsen A, Sibert J (2012) AD model builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software* 27:233–249
- Friedli J, Bacher S (2001) Direct and indirect effects of a shoot-base boring weevil and plant competition on the performance of creeping thistle, *Cirsium arvense*. *Biological Control* 22:219–226
- Godefroid S, Le Pajolec S, Hechelski M, Van Rossum F (2018) Can we rely on the soil seed bank for restoring xeric sandy calcareous grasslands? *Restoration Ecology* 26:S123–S133
- Halassy M (2001) Possible role of the seed bank in the restoration of open sand grassland in old fields. *Community Ecology* 2:101–108
- ter Heerdt GNJ, Verweij GL, Bekker RM, Bakker JP (1996) An improved method for seed-bank analysis: seedling emergence after removing the soil by sieving. *Functional Ecology* 10:144–151
- Kelemen A, Török P, Valkó O, Miglécz T, Tóthmérész B (2013) Mechanisms shaping plant biomass and species richness: plant strategies and litter effect in alkali and loess grasslands. *Journal of Vegetation Science* 24:1195–1203
- Kelemen A, Török P, Valkó O, Deák B, Miglécz T, Tóth K, Ölvedi T, Tóthmérész B (2014) Sustaining recovered grasslands is not likely without proper management: vegetation changes and large-scale evidences after cessation of mowing. *Biodiversity and Conservation* 23:741–751
- Kiehl K, Kirmer A, Donath T, Rasran L, Hölzel N (2010) Species introduction in restoration projects- evaluation of different techniques for the establishment of semi natural grasslands in central and northwestern Europe. *Basic and Applied Ecology* 11:285–299
- Király G (2009) *Újmagyar Fűvészkönyv. Magyarország hajtásos növényei*. [New Hungarian Herbal. The vascular plants of Hungary. Identification key.]. Aggtelek National Park Directorate, Jószaftó, Hungary

- Kiss R, Valkó O, Tóthmérész B, Török P (2016) Seed bank research in central-European grasslands—an overview. Pages 1–34. In: Murphy J (ed) Seed banks: types. Nova Science Publishers, Hauppauge, New York
- Kiss R, Deák B, Tóthmérész B, Migléc T, Tóth K, Török P, et al. (2020) Establishment gaps: biodiversity hotspots to support the colonization of target species in species-poor grasslands. *Restoration Ecology*. <https://doi.org/10.1111/rec.13135>
- Klaus VH, Hoefer CJ, Fischer M, Hamer U, Kleinebecker T, Mertens D, Schäfer D, Prati D, Hölzel N (2018) Contribution of the soil seed bank to the restoration of temperate grasslands by mechanical sward disturbance. *Restoration Ecology* 26:S114–S122
- Lengyel S, Varga K, Kosztyi B, Lontay L, Déri E, Török P, Tóthmérész B (2012) Grassland restoration to conserve landscape-level biodiversity: a synthesis of early results from a large-scale project. *Applied Vegetation Science* 15:264–276
- Lepš J (2004) Variability in population and community biomass in a grassland community affected by environmental productivity and diversity. *Oikos* 107:64–71
- Lukács BA, Török P, Kelemen A, Várbíró G, Radócz S, Migléc T, Tóthmérész B, Valkó O (2015) Rainfall fluctuations and vegetation patterns in alkaline grasslands—self-organizing maps in vegetation analysis. *Tuexenia* 35:381–397
- Miao R, Song Y, Sun Z, Guo M, Zhou Z, Liu Y (2016) Soil seed bank and plant community development in passive restoration of degraded sandy grasslands. *Sustainability* 8:581
- van der Mijnsbrugge K, Bischoff A, Smith B (2010) A question of origin: where and how to collect seed for ecological restoration. *Basic and Applied Ecology* 11:300–311
- Oliver TH, Heard MS, Isaac NJ, Roy DB, Procter D, Eigenbrod F, et al. (2015) Biodiversity and resilience of ecosystem functions. *Trends in Ecology and Evolution* 30:673–684
- Rayburn AP, Schriefer C, Zamora A, Laca EA (2016) Seedbank-vegetation relationships in restored and degraded annual California grasslands: implications for restoration. *Ecological Restoration* 34:277–284
- Šefferová Stanová V, Janák M, Ripka J (2008). Management of Natura 2000 habitats. 1530 *Pannonic salt steppes and salt marshes. European Commission, Brussels, Belgium
- Shang ZH, Yang SH, Wang YL, Shi JJ, Ding LM, Long RJ (2016) Soil seed bank and its relation with above-ground vegetation along the degraded gradients of alpine meadow. *Ecological Engineering* 90:268–277
- Skaug H, Fournier D, Nielsen A, Magnusson A, Bolker B (2016) glmmADMB: generalized linear mixed models using AD model builder. R package version 0.8.3.3. <http://glmmadmb.r-forge.r-project.org>. (accessed 19 Feb 2020)
- Tälle M, Deák B, Poschlod P, Valkó O, Westerberg L, Milberg P (2016) Grazing vs. mowing: a meta-analysis of biodiversity benefits for grassland management. *Agriculture Ecosystems and Environment* 15:200–212
- Tiley GE (2010) Biological flora of the British Isles: *Cirsium arvense* (L.) Scop. *Journal of Ecology* 98:938–983
- Török P, Deák B, Vida E, Valkó O, Lengyel S, Tóthmérész B (2010) Restoring grassland biodiversity: sowing low diversity seed mixtures can lead to rapid favourable changes. *Biological Conservation* 148:806–812
- Török P, Vida E, Deák B, Lengyel S, Tóthmérész B (2011) Grassland restoration on former croplands in Europe: an assessment of applicability of techniques and costs. *Biodiversity and Conservation* 20:2311–2332
- Török P, Migléc T, Valkó O, Kelemen A, Deák B, Lengyel S, Tóthmérész B (2012) Recovery of native grass biodiversity by sowing on former croplands: is weed suppression a feasible goal for grassland restoration? *Journal for Nature Conservation* 20:41–48
- Török P, Helm A, Kiehl K, Buisson E, Valkó O (2018) Beyond the species pool: modification of species dispersal, establishment and assembly by habitat restoration. *Restoration Ecology* 26:S65–S72
- Tóth K, Hüse B (2014) Soil seed banks in loess grasslands and their role in grassland recovery. *Applied Ecology and Environmental Research* 12: 537–547
- Valkó O, Tóthmérész B, Kelemen A, Simon E, Migléc T, Lukács B, Török P (2014) Environmental factors driving vegetation and seed bank diversity in alkali grasslands. *Agriculture, Ecosystems and Environment* 182:80–87
- Valkó O, Venn S, Zmihorski M, Biurrun I, Labadessa R, Loos J (2018) The challenge of abandonment for the sustainable management of Palearctic natural and semi-natural grasslands. *Hacquetia* 17:5–16
- Wagner M, Walker KJ, Pywell RF (2018) Seed bank dynamics in restored grassland following the sowing of high- and low-diversity seed mixtures. *Restoration Ecology* 26:S189–S199
- Walker KJ, Stevens PA, Stevens DP, Mountford JO, Manchester SJ, Pywell RF (2004) The restoration and re-creation of species-rich lowland grassland on land formerly managed for intensive agriculture in the UK. *Biological Conservation* 119:1–18
- Zuur A, Ieno E, Walker N, Saveliev A, Smith G (2009) Mixed effects models and extensions in ecology. Springer, New York

Supporting Information

The following information may be found in the online version of this article:

Table S1. The effect of management (mown/abandoned), grassland type (alkaline/loess), and their interaction on the vegetation and seed bank characteristics of the restored grasslands (generalized linear mixed models).

Table S2. Significant indicator species in the vegetation. Freq. refers to the total frequency of a species in the vegetation and seed bank samples ($N = 192$).

Table S3. Significant indicator species in the seed bank. Freq. refers to the total frequency of a species in the vegetation and seed bank samples ($N = 192$).