SOIL SEED BANKS IN LOESS GRASSLANDS AND THEIR ROLE IN GRASSLAND RECOVERY

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Abstract. Loess grasslands are among the most species-rich grasslands in Europe. In many regions only species-poor degraded fragments of formerly species-rich loess grasslands remained due to the agricultural intensification in the last century. To preserve and restore loess grasslands it is necessary to understand, how soil seed banks can contribute to the maintenance of diversity. We studied the vegetation and seed banks of (i) a loess grassland in a semi-natural state and (ii) a degraded loess pasture. We found that species richness was significantly lower in the degraded loess pasture (10.2 species/m^2) than in the semi-natural loess grassland (27.0 species/m^2). Mean seed bank densities were quite similar in the two grassland types (22,800 and 20,200 seeds/m^2, respectively). Out of the frequent graminoids in the vegetation, only *Poa angustifolia* possessed considerable dense seed banks. Forb species having considerable seed banks were mainly disturbance-tolerant species (e.g. *Euphorbia cyparissias*, *Galium verum* or *Hypericum perforatum*). Most characteristic forb species possessed only sporadic seed banks (e.g. *Filipendula vulgaris, Pimpinella saxifraga* and *Salvia nemorosa*). Our results suggest that seed banks have only a limited role in the recovery of loess grasslands.
Keywords: *grazing; grassland restoration; plant traits; propagule limitation, seed density*

Introduction

Grasslands contribute with a significant part to the biodiversity of Europe harbouring a very diverse flora and fauna at multiple spatial scales (Kovács-Hostyánszky et al., 2011; 2013; Valkó et al., 2012). The extension and diversity of grasslands is in a constant decline in Europe in the past decades, thus, conservation and restoration of species-rich grasslands is an urgent task nowadays (Penksza et al. 2010, 2013; Török et al., 2011, Házi et al. 2011, 2012; Szentes et al., 2011a, 2011b; Zimmermann et al., 2011, Kiss et al., 2011). For an effective planning of conservation, it is vital to understand mechanisms sustaining grassland biodiversity (Drobnik et al., 2011, Malatinszky et al. 2013, Valkó et al., 2013).

The maintenance and recovery of species diversity in grasslands can be supported by local propagule sources preserved in the form of persistent soil seed banks (Bossuyt & Honnay, 2008; Valkó et al., 2011). There are contrasting views on the role of soil seed banks in sustaining grassland biodiversity. Several studies stress that soil seed banks form an important source for re-colonization, especially when species dispersal is limited (Simmering et al., 2006). Persistent soil seed banks of characteristic grassland species enable fast grassland recovery after degradation or disturbances (Bossuyt & Honnay, 2008). However, other studies found that target species often lack persistent seed banks (Kalamees & Zobel, 1998; Bossuyt & Honnay, 2008). Still there is a shortage of seed bank records, especially for species of high conservational value. Underrepresentation of target species in databases might also hamper the understanding of seed banks' role in grassland recovery (Csontos, 2001; Valkó et al., 2011). To design

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conservation and restoration measures in grasslands it is necessary to study soil seed banks as potential propagule sources for grassland recovery.

The species composition and density of seed banks varies considerably across grassland types and regions, thus it is necessary to have seed bank analysis and persistency records for each grassland type of high conservation value. Published seed bank type records are available for approximately 50% of the Hungarian flora (Csontos, 2001). Hungarian seed bank studies were mainly published from sandy grasslands (Halassy, 2001; Matus et al., 2003, 2005; Török et al., 2009), mountain hay-meadows (Valkó et al., 2011), native alkali (Valkó et al., 2013) and restored alkali and loess grasslands (Török et al., 2012a), rocky grasslands on dolomite (Csontos et al. 1996a), oak forests and clearcuts (Csiszár 2004; Koncz et al., 2010, 2011; Csontos 2011), and pine plantations (Csontos et al. 1996b). Seed bank studies are especially crucial in very fragile and threatened species-rich steppic grasslands, like loess grasslands (Kelemen et al., 2013; Török et al., 2012b). The seed banks of loess grasslands were formerly studied by Virágh and Gerencsér (1998), but in this study for the detected species no seed bank classification was provided.

Loess grasslands are among the most species-rich communities in Europe and harbour many threatened plant and animal species (Török et al., 2011; Török et al., 2012b). The area of historically characteristic loess grasslands become fragmented in lowland areas in Central-Europe because of the agricultural intensification in the last century (Molnár and Botta-Dukát, 1998). In many regions, only species-poor degraded fragments of formerly species rich grasslands remained surrounded by croplands and other intensively managed agricultural lands (Török et al., 2012c, Vida et al., 2010). In spite of the high conservation value of loess grasslands, only sparse seed bank data is available for their characteristic species. To preserve and restore loess grasslands it is necessary to understand how soil seed banks can contribute to the maintenance of species diversity. A crucial question is whether target species already missing from aboveground vegetation of degraded stands are still present in the soil seed banks.

Aims of the study

In the present study, we evaluate the seed bank composition of two types of loess grasslands in relation with aboveground vegetation. Vegetation and seed bank composition of (i) a semi-natural loess grassland (Salvio nemorosae – Festucetum rupicolae) traditionally managed by mowing and (ii) a degraded, abandoned loess pasture (Cynodonti – Poëtum angustifoliae) were studied. We asked the following study questions: (i) How dense are the seed banks of loess grasslands? (ii) Which species of the vegetation possess persistent seed banks? (iii) Is the regeneration from seed banks feasible after degradation of loess grasslands?

Material and methods

Study sites

The studied grasslands are in the Hortobágy National Park (East-Hungary), near the village Hortobágy (Nyírőlapos, degraded loess pasture, N 47°34’47”, E 21°15’30”) and the town Balmazújváros (Magdolna Puszta, semi-natural loess grassland, N 47°35’01” E 21°17’54”). The vegetation in the region is characterised by alkali grasslands,

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scattered alkali marshes at the lowest and loess grassland patches at the highest elevations (Török et al., 2010, Kelemen et al., 2013). 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 yearly maximum precipitation is typical in June (mean 80 mm) with high year-to-year fluctuations (Molnár, 2004).

Nyírőlapos site was formerly an overgrazed species-poor loess pasture (Cynodonti – Poëtum angustifoliae) till the 1980's. We studied vegetation and seed banks of enclosures established in the 1980's, where no management have been applied.. Abandoned, degraded loess pastures (Cynodonti – Poëtum angustifoliae) are characterised by a high cover of grazing-tolerant grasses, sedges (*Cynodon dactylon*, *Poa angustifolia*, *Festuca pseudovina*, *F. rupicola* and *Carex stenophylla*) and forbs (*Convolvulus arvensis, Galium verum* and *Euphorbia cyparissias*). At heavily grazed sites, thistles dominate (*Eryngium campestre* and *Ononis spinosa*).

In the study region, only small stands of less degraded semi-natural loess grasslands (Salvio nemorosae – Festucetum rupicolae) have remained. The semi-natural grassland in Magdolna Puszta is one of these remnants. The site is traditionally managed by mowing. The characteristic grasses for species-rich loess grasslands are *Festuca rupicola*, *Bromus inermis*, *Koeleria cristata*, *Stipa capillata*, *Alopecurus pratensis* and *Poa angustifolia*. They are rich in perennial forb species, including several characteristic loess-specialist species (*Filipendula vulgaris, Fragaria viridis, Pimpinella saxifraga, Salvia nemorosa, Thymus glabrescens, Trifolium striatum* and *Veronica prostrata*).

Vegetation and seed bank sampling

In each grassland stand, twelve 1-m×1-m plots were marked randomly, and the percentage cover of vascular plants was recorded in June 2009. In the forthcoming spring (2010) three soil cores (4-cm in diameter and 10-cm in depth, 126 cm^3 per core,) were drilled from each plot for seed bank analyses (in total 36 soil cores per grassland). Two vertical segments (0-5-cm, 5-10-cm) were separated; then identical segments from the same plot were pooled. Samples were concentrated by sieving using the method of ter Heerdt et al. (1996). After bulk reduction, samples were spread in 3-4 mm thick layer on surface of trays filled with steam-sterilised potting soil. Germinated seedlings were regularly counted, identified and removed from the trays. Unidentified seedlings were transplanted and were grown until identification. Accidental airborne seed contamination was detected using sample-free control trays filled with steam-sterilised potting soil. Trays were placed in a greenhouse under natural light conditions and watered regularly from April to October. Watering was stopped in early July (when no seedlings emerged) to mimic natural drought conditions during summer. Watering was re-started in late August, and was continued until the early days of November.

Data processing and analysis

Species were grouped into 'graminoids' (i.e. Poaceae, Cyperaceae and Juncaceae) and 'forbs', i.e. dicots and non-graminoid monocots (including Typhaceae). Species were classified into seed bank types (SBT) based on the classification criteria of Csontos (2001) and Thompson et al. (1997). For seed bank types classification, we used vegetation records and vertical distribution data of the seed bank (seed density scores

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for the 0-5 and 5-10-cm layers). We assigned species to the following seed bank types: T – transient, SP – short-term persistent, LP – long-term persistent (Thompson et al., 1997). Seeds of transient species remain viable in the soil seed bank for less than one year, while seeds of persistent species can survive longer. Generally, short-term persistent seeds remain viable for 1-5 years, while long-term persistent ones can germinate even after being more than 5 years in the soil (Thompson et al., 1997). We assigned those species to SBT types which were either (i) present with at least 3 germinated seedlings (corresponding with a seed density of 66 seeds/m^2) or (ii) were detected in 50% of the plots in the aboveground vegetation (possessing frequency score of at least 6) in at least one grassland stand. Seedlings of *Carex praecox* and *C. stenophylla*; *Juncus bufonius* and *J. ranarius*; *Trifolium angulatum* and *T. retusum* and *Typha angustifolia* and *T. latifolia* were pooled because of identification difficulties. Greenhouse weeds detected in control trays were excluded from analyses. Means of species richness of grassland stands were compared using t-test (Zar, 1999). Similarity between the species composition of aboveground vegetation and seed banks was calculated by the Jaccard index. Vegetation and seed bank composition was compared using DCA ordination (Legendre and Legendre, 1998). Nomenclature follows Simon (2000) for taxa and Borhidi (2003) for syntaxa.

Results

Vegetation composition

We detected altogether 94 species in the vegetation and seed banks of the two study sites. We found altogether 58 species in the vegetation of the study sites: 24 species in the vegetation of degraded loess pasture and 52 species in the traditionally managed loess grassland, while 18 species were present in the vegetation of both study sites.

We detected significantly lower species numbers in the plots of the degraded loess pasture (Nyírőlapos – a mean of 10.2 species/m^2) than in the semi-natural loess grassland (Magdolna Puszta – a mean of 27.0 species/m^2; t-test, $p < 0.001$). The vegetation of the degraded loess pasture was characterised by the high cover of *Festuca rupicola;* only two other species possessed cover scores higher than 5% (*Galium verum* and *Poa angustifolia*; see *Table 1* and *Table 2*). Loess-specialist forb species (e.g. *Filipendula vulgaris* and *Salvia nemorosa*) were missing or only present with low cover scores in the degraded loess pasture (*Table 2*). The vegetation of the semi-natural loess grassland was also characterised by a high cover of *Festuca rupicola*, and there were four species present with cover scores higher than 5% (*Cynodon dactylon*, *Filipendula vulgaris*, *Poa angustifolia* and *Thymus glabrescens*). For detailed species composition, see *Figure 1*. In the DCA ordination, the aboveground vegetation and seed banks of the two loess grassland stands were clearly separated. A higher patchiness of species composition was detected both for the vegetation and seed banks of the degraded loess pasture compared to the semi-natural loess grasslands (*Figure 1*).

We detected altogether 68 species in the seed banks. In the seed bank of degraded loess pasture 52 species, in the semi-natural loess grassland 44 species were found, respectively. We detected 28 species in the seed banks of both study sites. We were able to classify 56 species into seed bank types (Thompson et al. 1997; *Table 1, Table 2*). Total density of seed banks in the two grassland types did not differ significantly; a mean seed density of 22,800 seeds/m^2 in the degraded loess pasture, and 20,200 seeds/m^2 in the semi-natural loess grassland were detected, respectively. No

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significant differences were found in seed bank species numbers in the two grassland types (means were 17.0 species/ m^2 in the degraded loess pasture and 15.4 species/ m^2 in the semi-natural loess grassland; t-test, P = 0.299). The Jaccard similarity of aboveground vegetation and seed banks were 0.31 in the degraded loess pasture and 0.35 in the semi-natural loess grasslands, respectively. In the degraded loess pasture 76%, while in the semi-natural loess grassland 46% percent of species detected in the aboveground vegetation possessed at least short-term persistent seed banks.

Table 1. *Percentage cover and seed density of graminoid species in the degraded (Nyírőlapos) and semi-natural (Magdolna Puszta) loess grasslands. Notations: VC: mean cover scores in the aboveground vegetation (%); VF: frequency scores in the aboveground vegetation; SN: seedling number; SF: frequency scores in the seed bank. SBT: seed bank type: T – transient, SP – short-term persistent, LP – long-term persistent (Thompson et al. 1997). One germinated seedling corresponds with a seed density of 22 seeds/m2. Species with a frequency score of more than six, or more than three germinated seedlings detected in one grassland stand were listed.*

	Degraded grassland				**Semi-natural grassland**				
	VC	**VF**	**SN**	**SF**	**VC**	**VF**	**SN**	**SF**	**SBT**
Agropyron intermedium					1.1	8			T
Agropyron repens	0.8	9							T
Alopecurus pratensis	0.5	6	7	1	0.4	2	2	2	T
Bromus mollis					0.2	9			T
Carex praecox/stenophylla			113	11	2.8	11	16	6	SP/LP
Cynodon dactylon	0.3	3			7	12	26	10	T
Echinochloa crus-galli							5	1	LP
Festuca rupicola	44.6	11	5	3	33.9	12	31	8	SP
Juncus bufonius/ranarius			5	4			6	4	LP
Juncus compressus			9	6			45	8	LP
Koeleria cristata	0.1	1			0.6	7	6	4	T
Poa angustifolia	7.2	11	43	11	6.1	11	48	11	SP

Out of the most frequent species in the vegetation of the degraded loess pasture, only two forbs, *Galium verum* (4268 seeds/m^2) and *Achillea collina* (2090 seeds/m^2) possessed considerable dense seed banks (higher seed density than 1000 seeds/m^2; *Table 2*). Graminoids present in the aboveground vegetation with high cover scores (like *Festuca rupicola* and *Poa angustifolia*) possessed only low-density seed banks (*Table 1*). Several species sporadically found in the aboveground vegetation, possessed dense seed banks in the degraded loess pasture, like some short-lived weeds (*Carduus acanthoides*, 860 seeds/m^2 and *Conyza canadensis*, 6764 seeds/m^2), sedges (*Carex praecox* and *C. stenophylla*, 2486 seeds/m^2) and wind-dispersed hygrophytes (*Epilobium tetragonum*, 575 seeds/m^2). Loess-specialist forbs detected with low cover scores in the vegetation possessed only sparse (*Salvia nemorosa*, 66 seeds/m^2) or no seed banks (*Filipendula vulgaris*).

Among the most frequent graminoids in the vegetation of the semi-natural loess grassland, only *Poa angustifolia* possessed considerable seed banks (1061 seeds/m^2). Other frequent graminoids of the aboveground vegetation possessed lower seed densities (e.g. *Festuca rupicola* - 685 seeds/m^2, *Cynodon dactylon* - 545 seeds/m^2; *Table 1*). In the seed bank of the semi-natural loess grassland, eight forb species had

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higher seed density than 500 seeds/m^2; these were *Euphorbia cyparissias* (685 seeds/m^2), *Hypericum perforatum* (6,233 seeds/m^2), *Myosotis stricta* (1,967 seeds/m^2), *Plantago lanceolata* (1,017 seeds/m^2), *Potentilla arenaria* (1,304 seeds/m^2), *P. argentea* (1,326 seeds/m^2), *Stellaria graminea* (862 seeds/m^2) and

***Table 2**. Percentage cover and seed density of forb species in the degraded (Nyírőlapos) and semi-natural (Magdolna Puszta) loess grasslands. For notations, see Table 1.*

	Degraded grassland				**Semi-natural grassland**				
	VC	**VF**	**SN**	**SF**	**VC**	**VF**	**SN**	**SF**	**SBT**
Achillea collina	2.6	8	95	11	1.7	10	11	6	SP
Arenaria serpyllifolia			7	4					LP
Carduus acanthoides	0.1	4	39	12	0.1	1	2	2	SP
Centaurium minus			4	1					LP
Chenopodium album			5	2			1	1	LP
Chenopodium strictum			4	3					LP
Cirsium arvense			5	4					LP
Convolvulus arvensis	0.2	5	4	2	0.1	4			T/LP
Conyza canadensis	0.1	1	307	12					SP/LP
Cruciata pedemontana			8	2	0.1	2			T/LP
Cynoglossum officinale	1.7	8	5	2					T
Daucus carota			2	2	0.7	9	3	3	T
Epilobium tetragonum	0.1	1	26	9			6	3	SP
Euphorbia cyparissias	0.2	5	4	3	0.3	6			T/SP
Filipendula vulgaris	0.4	12			5.5	12			T
Fragaria viridis	1.1	8	3	1	7	11	1	1	T
Galium verum	22.9	12	194	10	4.4	11	3	2	SP
Gypsophila muralis			13	6			7	5	LP
Hypericum perforatum					0.3	5	283	12	SP
Inula britannica	0.1	1	8	2	0.1	3	1	1	SP
Lotus corniculatus					0.6	7	4	3	T
Medicago falcata					1.6	7			T
Medicago lupulina			2	2			5	5	LP
Myosotis stricta			20	5	0.1	4	89	12	SP/LP
Pimpinella saxifraga					1.2	8			T
Plantago lanceolata					0.5	10	46	10	SP
Polygonum aviculare	0.1	2	6	4	0.1	1	6	4	SP/LP
Potentilla arenaria	0.1	2	8	4	1.3	12	59	12	SP
Potentilla argentea	0.2	4	4	3			60	11	LP
Salvia nemorosa	3.6	7	3	3	5.2	11			T
Sonchus asper			6	3					LP
Stellaria graminea	2.6	4	1	1	0.1	1	39	11	T/SP
Thymus glabrescens					7	12	3	3	T
Trifolium angulatum/retusum			8	4					LP
Trifolium striatum			5	3	0.6	6			T/LP
Typha angustifolia/latifolia			4	1			8	5	LP
Verbascum phoeniceum			9	4	1.3	12	10	4	SP/LP
Veronica persica			22	6			55	12	LP
Veronica prostrata			1	1	0.6	8	1	1	T
Veronica verna					0.3	10			T
Vicia angustifolia					0.5	6			T
Vicia lathyroides					0.4	4	13	8	SP

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Veronica persica (1,216 seeds/m^2). Several forb species characteristic to loess grasslands like *Knautia arvensis*, *Pimpinella saxifraga*, and *Salvia nemorosa* had no or at most very sparse seed banks (*Table 2*).

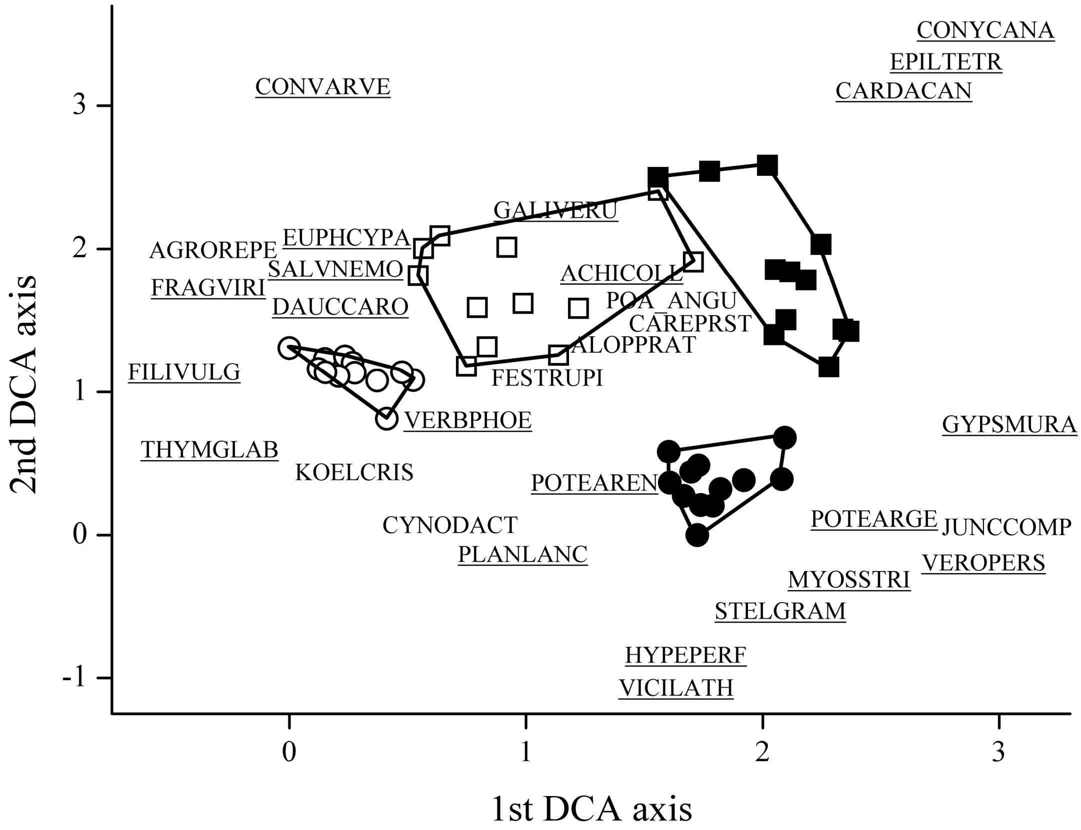

Figure 1**. Species composition of vegetation and seed banks of the studied grasslands displayed by a DCA ordination based on presence-absence datasets. Notations: □ – degraded loess pasture, vegetation; ■ – degraded loess pasture, seed bank; ○ – semi-natural loess grassland, vegetation; ● – semi-natural loess grassland, seed bank. The most frequent 30 species are shown, using four letters of their genus and four letters of their species names. Forbs were marked with underlines.* ***Seed bank composition

Discussion

Seed banks of loess grassland species

No significant differences were found between the mean seed bank densities of the two types of loess grasslands. Seed bank densities were higher than in other species-rich dry grassland types, like dry calcareous grasslands (200-900 seeds/m^2; Bossuyt et al., 2006 Kalamees and Zobel, 1998) or chalk grasslands (6000-7000 seeds/m^2; Poschlod and Jackel, 1993).

We found that most characteristic species of loess grasslands possessed at most sparse seed banks. For most of the characteristic graminoids in the aboveground vegetation, persistent seed banks were not detected in the two types of loess grasslands. Former seed bank studies in grasslands found that in case of perennial grasses, seed bank formation is often subordinated to clonal reproduction (Bossuyt and Honnay, 2008). In our study, the only perennial grass species with considerable seed densities

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was *Poa angustifolia*. This generalist grass species was found in high desities in several grassland types (e.g. sandy grasslands, Török et al., 2009), or restored secondary grasslands (Török et al., 2012a).

We found that forb species typical in the aboveground vegetation of the semi-natural loess grassland (e.g. *Fragaria viridis*, *Salvia nemorosa* and *Thymus glabrescens*) possessed no or only sparse seed banks in both loess grassland types. Forb species with considerable seed banks were mainly disturbance-tolerant species (*Euphorbia cyparissias*, *Galium verum*, *Hypericum perforatum* and *Potentilla argentea*).

Similarity of vegetation and seed banks

In former studies, low to medium similarity was found between vegetation and seed banks in temperate grasslands (Bossuyt & Honnay, 2008; Hopfensperger, 2007). This result was also supported by our study: mean Jaccard similarity scores were raging between 0.31 and 0.35 in the studied grassland types. There are several explanations for this phenomenon: (i) Perennial grasses of the aboveground vegetation often lack persistent seed banks (Bakker et al., 1996, Bekker et al., 1997). (ii) Seed banks are mainly characterised by weedy and disturbance-tolerant species missing or underrepresented in the aboveground vegetation in most semi-natural grasslands (Valkó et al., 2011). (iii) For rare species with aggregated seed banks, the probability of detection is low (Thompson et al., 1997). (iv) There is also a high chance for non-detection of short-lived species with high fluctuations in aboveground cover (Török et al., 2009).

Implications for restoration

Loess grasslands are among the most fragile and vulnerable grasslands harbouring high species diversity (Somodi et al., 2008). In a recent study, Kelemen et al. (2013) found that loess grasslands are especially threatned by degradation, because even a slight change in total biomass production can result in a decrease of species richness in these grasslands. Abandonment or inappropriate management by overgrazing alter biomass conditions in loess grasslands, leading to fewer and less suitable microsites for the germination and establishment of target species (Deák et al., 2010; Miglécz et al., 2013). Our results suggest that the local seed banks have only a minor contribution to the maintenance of diversity in both degraded and semi-natural loess grasslands. Irrespective of the state of degradation, only a small number of species characteristic to loess grasslands built up detectable seed banks. Therefore, loess-specialist species can become locally extinct if they disappear from the aboveground vegetation. Restoration of former species richness is therefore not possible from local seed banks in loess grasslands. Our results underline the importance of the traditional management for the species-rich loess grasslands.

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