



Recovery of native grass biodiversity by sowing on former croplands: Is weed suppression a feasible goal for grassland restoration?

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ABSTRACT

Grassland restoration on former croplands offers good opportunity to mitigate the loss of grassland biodiversity. Weed suppression can be another benefit, which becomes increasingly important because of the high recent rate of abandonment of arable lands in Central and Eastern Europe. Our aim was to evaluate the usefulness of sowing two low-diversity seed mixtures followed by annual mowing, a frequently used restoration technique, in weed suppression. We found that rapidly forming cover of sown grasses effectively suppressed short-lived weeds and their germination except in the first year. The detected dense seed bank of short-lived weeds points out the possibility and threat of later weed infestation. In the short run perennial weeds cannot be suppressed easily by sowing and annual mowing. We found that the effectiveness of seed sowing followed by mowing in weed suppression can be different on sites with different history or seed mixture. Rapidly establishing perennial weeds, such as *Agropyron* species were only detected in former alfalfa fields; *Cirsium arvense* was found in former cereal and sunflower fields but not in former alfalfa fields. We found that the rate of weed suppression and success was influenced by the seed mixtures used. In several alkali restorations the high proportion of perennial weeds was detected in year 3. In loess restorations, much lower scores were typical. This was likely caused by the different seed mixture used. The loess seed mixture contained seeds of a clonally spreading tall-grass, *Bromus inermis*, which could compete more effectively with clonally spreading weeds, than could short grass species with or without tussock forming. Our findings indicate that post-restoration management require carefully designed actions that are fine-tuned addressing specific threats at the site level.

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Introduction

Grassland restoration in former arable lands offers a great opportunity to mitigate the overall loss of grassland biodiversity (Ewers & Didham 2005; Plieninger & Gaertner 2011; Römermann et al. 2005). Grassland restoration can be used to establish novel grasslands, increase the area of grassland fragments, and to create connections between, and buffer zones around, grassland fragments (Critchley et al. 2003). Thus, negative influences from surrounding agricultural areas (like infiltration/runoff of chemicals, and human disturbance) can be reduced (Karlík & Poschold 2009; Török et al. 2010). Weed control can be another benefit of restoration, especially in areas such as abandoned croplands, roadsides, and field margins (Blumenthal et al. 2005). Weed control is becoming increasingly important because of the recent high rate of abandonment of agricultural areas in Central and Eastern Europe,

and elsewhere (Cramer et al. 2008; Pullin et al. 2009), which can present substantial management problems. It is often a high priority to control weeds in abandoned areas to avoid weed infestation of natural habitats and agricultural fields and to slow their spread in the landscape (Blumenthal et al. 2003). Given the generally high costs of weed control interventions, the potential weed control benefit of grassland restoration can be a powerful argument to convince decision makers to fund grassland restoration worldwide.

Agricultural weed species as 'ruderal strategists' are generally characterised by high growth rates, short life spans and high reproductive allocation in the form of large amounts of persistent seeds (Bekker et al. 1997; Thompson et al. 1997). Weeds can rapidly establish in abandoned croplands already having vegetative propagule banks (e.g. tillers or rhizomes) and/or seed banks in the soil (Grime 1979; Prach et al. 2007). Weeds are often successful competitors in crop fields where high levels of soil nutrients are available but usually poorly adapted to late successional competitive environments (Blumenthal et al. 2005; Török et al. 2008). This observation raises the possibility that restoration using a direct sowing of late successional competitor species may be useful in

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weed control. Although grassland restoration by seed sowing is often recommended, especially in sites where weed domination is foreseen (Hedberg & Kotowski 2010; Prach & Hobbs 2008), the effectiveness of sowing in weed suppression was analysed only in a few studies (e.g. Lepš et al. 2007; Van der Putten et al. 2000).

We studied the short-term vegetation dynamics and soil seed banks of grasslands restored by sowing low-diversity seed mixtures on former croplands. Our aim was to evaluate the usefulness of a frequently used restoration technique, i.e., sowing low-diversity seed mixtures followed by yearly mowing, in the recovery of grass biodiversity and weed control. We particularly asked the following questions: (i) Which weed species groups are likely to be suppressed by this way of restoration? (ii) How is weed suppression influenced by previous site history and the different seed mixtures? (iii) Can the success of weed suppression be compromised by the re-establishment of weed vegetation from soil seed banks?

Methods

Study sites

The study site is located in the Hortobágyi National Park (Egyek-Pusztakócsi mocsarak, east Hungary, N 47° 34', E 20° 55'). The climate of the study site is continental with a mean annual precipitation of 550 mm (high yearly fluctuations occur frequently), and a mean temperature of 9.5 °C. A landscape-level grassland restoration project was started in the study region in 2005 (<http://life2004.hnp.hu>). Two low-diversity seed mixtures of native grasses were sown on 17 former crop fields (10 alfalfa, four sunflower and three cereal fields, 200 ha total) after seed bed preparation (deep ploughing and smoothing) in October 2005 (11 fields) and 2006 (six fields). The 'alkali' seed mixture containing seeds of *Festuca pseudovina* (67%) and *Poa angustifolia* (33%) were sown in nine fields, whereas the 'loess' mixture with the seeds of *Festuca rupicola* (40%), *Bromus inermis* (30%) and *Poa angustifolia* (30%) were sown in eight fields. The seed mixtures were sown at 25 kg per hectare in accordance with former restorations where similar amounts of seeds were sown (please see Kiehl et al. 2010; Török et al. 2011a). After sowing, the fields were regularly mown once in early June each year, before the seed ripening peak of most weed species, and the mown hay was removed from the area. No other management tool was used.

The soil of the studied fields was moderately compact (loam or clay-loam), with a pH (H₂O) of 6.0–7.6, and characterised by low salt (<0.02%) and CaCO₃ (<2%) contents. In all fields high phosphorous (typically 500–700 mg/kg) and potassium (typically 400–600 mg/kg) contents were measured, which frequently occurs after long-term crop production.

Study design and sampling

One sampling site (5 m × 5 m) per restored field was designated randomly but avoiding the field margins. In every sampling site, four 1 m × 1 m plots were permanently marked. In the plots, the cover of vascular plant species was recorded in early June before mowing in the three years after the sowing. For vegetation reference we selected typical stands of native alkali (*Achilleo setaceae-Festucetum pseudovinae*, three stands) and loess grasslands (*Salvio nemorosae-Festucetum rupicolae*, three stands) within a 20 km radius of the sown fields. We used the same sampling design for vegetation recording as described above.

Seed bank of sown grasslands was sampled in the third year after the sowing when the perennial cover was closed. Samples were collected after natural winter stratification and snowmelt in the plots for vegetation recording, in late March of 2008 (11 fields)

and 2009 (six fields). We bored three soil cores per plot (4 cm in diameter, 10 cm in depth, 126 cm³/core, and altogether 12 cores per sampling site); 204 soil cores in total. Cores from the same plot were pooled to reduce sample heterogeneity. Sample volume was reduced by 60–80% by the sample concentration 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 removed using a 0.2-mm-fine mesh. Concentrated samples were spread in a thin layer (maximum thickness about 3–4 mm) on trays, previously filled with steam-sterilised potting soil. Trays were placed under natural light in a greenhouse shaded from early May to August. Seedlings were regularly counted, identified then removed. Unidentified plant specimens were transplanted and grown until they could be identified. In early July, when no seedlings emerged, regular watering was stopped, and the dried sample layers were crumbled and turned. In early September, watering was re-started and continued until early November. Occasional seed contamination (e.g. dispersal by wind) was monitored in sample-free control trays filled with steam-sterilised potting soil.

Data processing

Vegetative individuals of *Agropyron repens* and *A. intermedium* were difficult to distinguish, so their scores were pooled as *Agropyron* sp. during the data analyses. Similarly, seedlings of *Typha angustifolia* and *T. latifolia* were pooled as *Typha* sp. in all analyses.

Weed species were selected based on Grime's ruderal species group (1979), as adapted to local conditions in the Social Behaviour Types general classification of Borhidi (1995) and fine tuned by the personal expertise of the authors in alkali and loess vegetation. The species groups AC (adventive competitors, e.g. *Conyza canadensis*, *Ambrosia artemisiifolia*), RC (ruderal competitors, e.g. *Cirsium arvense*, *Agropyron repens*) and W (mostly annual and biannual weedy grasses and forbs of low competitiveness) were considered as weeds. We classified all detected species into functional groups based on simplified life-form categories (*short-lived*: Th, TH and *perennial*: H, G, Ch) and morphological features (*graminoids* = Juncaceae, Cyperaceae and Poaceae, and *forbs*). Differences in vegetation mean cover and species richness scores between years were analysed using ANOVA with repeated measures (RM) followed by Tukey tests for mean comparison (Zar 1999). DCA ordination was based on the percentage cover of the species using CANOCO 4.5 (ter Braak & Šmilauer 2002). Nomenclature follows Simon (2000) for taxa and Borhidi (2003) for syntaxa.

Results

Vegetation changes

Temporal vegetation development is represented by the first axis in Fig. 1. The first year vegetation characterised by short-lived species was gradually replaced by a perennial vegetation dominated by sown grasses in most sites. By the third year, vegetation records of the alkali and loess restorations are clearly separated. There was also a separation between the point cloud representing the third year vegetation of alkali restorations of former alfalfa fields and that representing the third year vegetation of former cereal and sunflower fields. The third year vegetation records of several sown fields are close to the reference grasslands.

We detected a total of 113 species (incl. 47 weeds) in the vegetation of sown fields during the three years of study. Only 34 of these species had more than 5% cover in at least one field and year (Appendix A). The mean total species richness and the species richness of short-lived weeds was highest in the first year and thereafter a tendency to decrease was typical both in alkali (Table 1, RM

Table 1

Species richness and cover scores of short lived-weeds and cover (mean ± SE, %) of sown grasses in fields sown with alkali and loess seed mixtures. Different superscripted letters indicate significant differences between years (RM ANOVA and Tukey test, $P < 0.001$, $N = 9$ for alkali, and $N = 8$ for loess fields, respectively).

	Year 1	Year 2	Year 3
Alkali restorations			
Total species richness	15.3 ± 1.1 ^a	9.7 ± 1.4 ^b	6.8 ± 0.9 ^b
Species richness of short lived weeds	8.1 ± 0.7 ^a	3.3 ± 0.8 ^b	1.3 ± 0.5 ^b
Cover proportion of sown grasses	22.6 ± 7.6 ^a	54.7 ± 11.3 ^b	67.6 ± 5.8 ^b
Cover proportion of short-lived weeds	64.2 ± 9.9 ^a	18.5 ± 6.8 ^b	1.7 ± 0.6 ^b
Loess restorations			
Total species richness	15.4 ± 0.5 ^a	9.0 ± 1.0 ^b	8.1 ± 0.6 ^b
Species richness of short lived weeds	7.8 ± 0.6 ^a	2.0 ± 0.4 ^b	1.0 ± 0.3 ^b
Cover proportion of sown grasses	16.0 ± 5.0 ^a	76.5 ± 6.8 ^b	86.7 ± 3.2 ^b
Cover proportion of short-lived weeds	69.6 ± 8.5 ^a	4.3 ± 1.2 ^b	1.8 ± 0.6 ^b

ANOVA, $N = 9$, $F = 20.9$ and 39.3 for total and weed species richness, respectively, $P < 0.001$) and loess restorations (RM ANOVA, $N = 8$, $F = 32.8$ and 101.3 , respectively, $P < 0.001$). A high cover of short-lived weeds was detected in almost every field in the first year (for frequent species see Fig. 1, and for more detailed changes see Appendix A). After the first year, a sharp decline in the cover of short-lived weeds was typical, in parallel with an increase of sown grass cover, which was detected in every field (RM ANOVA, for alkali restorations: $N = 9$, $F = 37.6$ and 25.5 for weed and sown grass cover, respectively, $P < 0.001$; and for loess restorations: $N = 8$, $F = 60.6$ and 67.5 , respectively, $P < 0.001$; Appendix A). By the third year, perennial species became dominant (mostly perennial sown grasses) in every field.

In several fields a considerable cover of a few species of perennial weeds was detected which were not found as considerable cover in native target grasslands (Appendix B). In most alkali restorations on alfalfa fields, a high or increasing cover of perennial weedy *Agropyron* species was typical (Appendix A). In fields alfalfa-alkali-1 and alfalfa-alkali-2 the cover of *Agropyron* species was increased

during the three years (RM ANOVA, $N = 4$, the detected increase was significant for alfalfa-alkali-1: $P < 0.001$, $F = 25.83$). In most of the former cereal and sunflower fields sown with alkali seed mixture a high cover of *Cirsium arvense* was detected. *Cirsium arvense* cover increased continuously in fields cereal-alkali-2, sunflower-alkali-1 to 3 from year 1 to year 3 (significantly in cereal-alkali-2: RM ANOVA, $N = 4$, $F = 7.59$, $P = 0.023$, and marginally significantly in sunflower-alkali-1: $F = 4.12$, $P = 0.079$). Conversely, in most loess restorations either a low cover (typically lower than 5%) or a decreasing cover of perennial weeds was detected after the first year regardless of site history (e.g. cereal-loess-1 first year cover of $35.1 \pm 1.8\%$ decreased to $15.8 \pm 3.6\%$ to year 3; mean ± SE). However, in field cereal-loess-1, the cover of *Cirsium arvense* increased with high fluctuations from $7.1 \pm 3.4\%$ in 1 year to $14.8 \pm 3.3\%$ to year 3.

Seed bank and vegetation

A total of 3,802 seedlings of 76 species were counted and removed during the study. The mean total seed bank density ranged from 4,775 to 23,741 seeds/m². Most scores were typically within the range of 11,000 and 18,000 seeds/m². Out of the 21 most frequent species of the seed bank, there were 13 weed species, represented by 2,740 seedlings (almost 70% of total seed bank density, a mean seed density of 2,800–20,500seeds/m²). We found considerably dense seed banks of short-lived weed species in all fields regardless of site history or seed mixture (Appendix C). The most frequent seed bank species, *Capsella bursa-pastoris*, was detected in almost all fields with high density; the highest scores were typical in former alfalfa fields. Conversely, *Echinochloa crus-galli* was more frequent in soils of former cereal and sunflower fields, and only a few of its seeds were found in former alfalfa fields. For most of the weed species no such clear trends were found. Only a few non-weedy forbs had a considerable dense seed bank. *Gypsophila muralis* and *Matricaria chamomilla*, characteristic short-lived pioneers of alkali grasslands showed high density only in alkali restorations on former alfalfa and cereal fields. Seeds of wind-dispersed and small seeded hygrophites (such as *Typha* sp. and *Epilobium tetragonum*) were found in every sown field. The sown grasses had mostly sporadic seed banks, only *Poa angustifolia* had considerably dense seed banks (up to 1,260 seeds/m²). We found mostly low-density seed banks of perennial weedy forbs (typically up to a few hundred seeds/m²), and no seed banks were found for perennial weedy graminoids (Appendix C).

In the vegetation and seed bank altogether 146 species were found. Species composition of the seed bank showed the highest similarity with the species composition of the vegetation of the first year (Jaccard similarity ranged from 0.16 to 0.38). The mean scores of similarity significantly decreased from year 1 to year 3 in both types of seed mixtures (RM ANOVA, $P < 0.001$, alkali restorations, $N = 9$, $F = 13.53$; loess restorations, $N = 8$, $F = 19.93$). Several

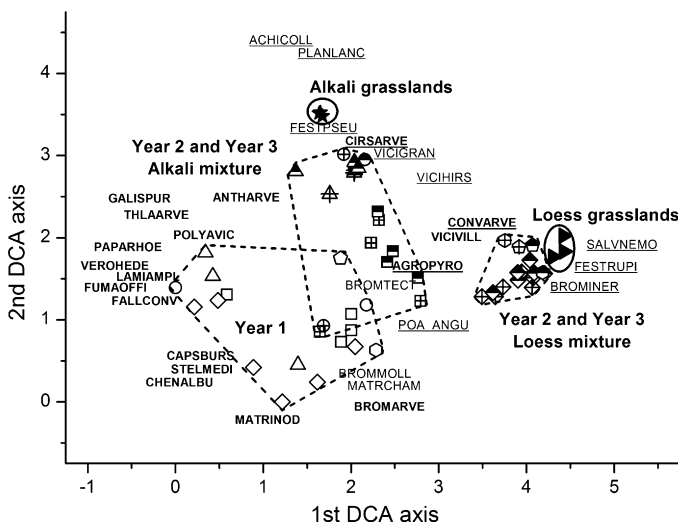


Fig. 1. Vegetation development in former alfalfa, cereal and sunflower fields sown with low-diversity seed mixtures towards reference grasslands as shown by a DCA ordination (eigenvalues for 1st and 2nd axis are 0.71 and 0.46, while gradient lengths are 4.42 and 3.53, respectively). Cumulative species variances for 1st and 2nd axis are 12.5 and 20.5, respectively). Notations: Alfalfa fields with alkali mixture = Year 1: □, Year 2: ▢, Year 3: ▣. Sunflower fields with alkali seed mixture = Year 1: △, Year 2: ▴, Year 3: ▾. Cereal fields with alkali seed mixture = Year 1: ○, Year 2: ⊕, Year 3: ⊙. Alfalfa fields with loess seed mixture = Year 1: ◇, Year 2: ⊕, Year 3: ⊙. Sunflower fields with loess mixture = Year 1: ○, Year 2: ⊕, Year 3: ⊙. Cereal fields with loess mixture = Year 1: ○, Year 2: ⊕, Year 3: ⊙. Reference alkali grasslands: ★. Reference loess grasslands: ▶. The most frequent 30 species were denoted by a combination of four letters of genus and four letters of species names like the following example: CHENALBU = *Chenopodium album* (but excl. *AGROPYRO* = *Agropyron* sp.). Perennial species were denoted with underline, weeds with boldface.

short-lived weed species that were detected with a high cover in first-year vegetation and suppressed later had a considerably dense seed bank (e.g. *Capsella bursa-pastoris*, *Matricaria inodora*). Some other short-lived weeds such as *Fumaria officinalis*, *Fallopia convolvulus*, *Bromus arvensis*, *Papaver rhoeas*, *Veronica hederifolia* possessed only very sporadic seed banks. Conversely, several short-lived weed species detected with very low cover had considerably dense seed banks (*Echinochloa crus-gallii*, *Setaria glauca*, and *S. viridis*).

Discussion

Grassland recovery and weed suppression

We found contrasting short-term success of weed suppression in our study in relation to specific life history traits. Short-lived weeds (both forbs and graminoids) were effectively suppressed by sowing low-diversity seed mixtures and mowing as part of a post-restoration management in every sown field. The cover scores of short-lived weed species were reduced from a mean of 64–67% in year 1 to a mean around 2% in year 3. Similar results were detected in other grassland restoration studies using low or high-diversity seed mixtures (Critchley et al. 2006; Jongepierová et al. 2007; Lawson et al. 2004; Lepš et al. 2007). Short-lived weeds are easily suppressed because of their (i) poor competitive ability (Tilman 1982), (ii) missing persistent seed banks, as was found for several species in this study, (iii) germination failure by a physical barrier or shading by both accumulated litter and green biomass (Van der Putten et al. 2000), and also germination inhibition by discharged allelochemicals (Ruprecht et al. 2008).

We found that basic grass diversity can be recovered within three years in most of the sown fields by the grassland restoration method; but in some fields even the recovery of basic grass diversity was delayed by weedy perennials which could not be suppressed by the used restoration procedure in the short run. The most persistent perennial weeds in our study were *Agropyron repens*, *A. intermedium* and *Cirsium arvense*. These species were also identified as problem plants in several other studies, where their increased dominance was detected after seed sowing (*Agropyron repens*, Lepš et al., 2007), during spontaneous grassland recovery in old-fields (*Agropyron repens* and *Cirsium arvense*, Prach et al. 2007; Prach & Pyšek, 2001; Ruprecht 2005, *A. intermedium*, Török et al., 2011b), and in several managed agricultural areas (*Cirsium arvense*, De Bruijn & Bork 2006). In a sowing experiment using regional seed mixtures in a density of 20 kg/ha Jongepierová et al. (2007) a significant increase of several perennial weeds was found (e.g. *A. repens* and *Taraxacum* sect. *ruderalia*) similarly to our findings.

These perennials have an effective clonal reproduction and vegetative spreading strategy by lateral tillers, so they can survive soil preparation and sowing practices and can rapidly establish through vegetative spreading by tillers (Lepš et al. 2007; Prach et al. 2007). This was also suggested by Pywell et al. (2003), where the performance of a species in restoration in former croplands was significantly favoured if the species was capable of effective vegetative growth and spreading. In addition to vegetative spreading, we found that *Cirsium arvense* can have a considerably dense seed bank (e.g. 1,790 seeds/m² in this study) and its seeds can be effectively dispersed by wind and secondarily by ants from nearby seed sources (Albrecht 2005; De Bruijn & Bork 2006; Lengyel et al. 2010). The rapidly increased cover of perennials detected in our study can be also supported by high nutrient levels in the soil, which is a result of previous use of fertilisers common in crop production. To suppress these perennial weeds, more intensive management practices are necessary. Increased mowing frequency (for *Agropyron repens*, Parr & Way 1988) or high-density rotational grazing

by cattle (for *Cirsium arvense*, De Bruijn & Bork 2006) can be more proper solutions for decreasing the cover of the perennial weeds detected.

Finally, in agricultural practice, sowing densities of 80–100 kg/ha or even higher (up to 500 kg/ha) are frequently used (van Andel & Aronson 2006), which is much higher than the density in this study (25 kg/ha). High-density sowing results in a dense grass sward, which may suppress weeds more effectively than low-density sowing, but may also hamper later immigration of the targeted subordinate species (Hellström et al. 2009).

Seed mixtures and site history

We found that the effectiveness of seed sowing followed by mowing in weed suppression can be different on sites with different history or seed mixture used. Contrasting success was found in our study in fields with different previous crop but same seed mixture sown. Rapidly establishing perennial graminoid weeds, such as *Agropyron* species were detected only in former alfalfa fields. Conversely, the perennial weedy forb *Cirsium arvense* was found in former cereal and sunflower fields but not in former alfalfa fields. The absence of perennial weedy forbs in former alfalfa fields can be related to the cultivated alfalfa, which itself is a perennial forb and can effectively suppress other weeds (incl. *Cirsium arvense*), as was shown in a previous study of ours (Török et al. 2011b). In that study, at most low cover of *Cirsium arvense* was detected in former alfalfa fields and the perennial alfalfa cover was gradually replaced by perennial grass cover without the stage dominated by perennial weedy forbs. In several other studies, remarkably high cover of *Cirsium arvense* was reported from cereal and maize fields (the latter are cultivated similarly as sunflower), which agrees well with our finding of high cover of *Cirsium* in most of our former cereal and sunflower fields (De Bruijn & Bork 2006; Gerowitt 2003; Jongepierová et al. 2004; Romero et al. 2008). These results clearly indicate that planning restoration efforts for different seed mixtures or fields with different previous crop may require the plan of different restoration measures for the same rate of success.

It was found formerly that the recovery of grassland vegetation in former croplands can be influenced by several constraints depending on site history such as (i) impoverished local propagule sources and/or dispersal limitation of grassland species (Bekker et al. 1997; Bissels et al. 2006; Valkó et al. 2011), (ii) unsuitable soil conditions, e.g. higher nutrient levels (Pywell et al. 2002) and (iii) increased availability of vegetative and generative propagule-bank of weeds (Bekker et al. 1997; Hutchings & Booth 1996). In seed sowing experiments, knowing this information constrains elimination of the seed limitation of grassland species and suppressing weeds by sowing and/or with topsoil removal recommended (Critchley et al. 2006; Klimkowska et al. 2010; Pywell et al. 2002; Török et al. 2011b).

In several alkali restorations in this study, the proportion of perennial weeds increased during the three years of vegetation development, and was high in year 3. In loess restorations, much lower scores were typical. This was likely caused by the different seed mixture used. The loess seed mixture contained seeds of a clonally spreading tall-grass, *Bromus inermis*, which could probably compete more effectively with clonally spreading *Cirsium arvense* or *Agropyron repens*, than could short grass species with or without tussock forming like *Poa angustifolia* or *Festuca pseudovina* (e.g. Pywell et al. 2003).

Seed banks

We found that several short-lived weeds that were effectively suppressed (e.g. *Capsella bursa-pastoris*, *Matricaria inodora*) or not even detected in aboveground vegetation (e.g. *Setaria viridis*, *S.*

	FSG	AA1	AA2	AA3	AA4	CA1	CA2	SA1	SA2	SA3	AL1	AL2	AL3	AL4	AL5	AL6	CL1	SL1
<i>Festuca rupicola</i>	PG										4.5	0.7	0.9	3.5	3.1	0.6	5.4	15.3
<i>Poa angustifolia</i>	PG	0.8	54.0	39.3	22.0	32.4	1.5	1.9		0.5	17.4	3.9	0.1	6.5	1.2	0.6	3.4	11.2
Year 2																		
Anthemis arvensis	SF								14.8	40.1								
Capsella bursa-pastoris	SF	32.1	5.0				7.5	0.4	1.7	2.4						1.8		
Matricaria inodora	SF	11.4	1.0	0.1			24.5	5.1	0.9	3.8	0.9	0.4	0.1			0.6	0.1	0.2
<i>Medicago lupulina</i>	SF									0.1					0.7	0.9	18.8	
<i>Trifolium angulatum</i>	SF						1.6	8.1	0.1	0.3								0.1
<i>Vicia hirsuta</i>	SF			0.4	0.1	0.9		9.7	10.1	10.5	0.3			0.1		0.2	6.5	36.8
<i>Vicia grandiflora</i>	SF									26.8								
Vicia villosa	SF				0.1					1.3	5.4	0.5					7.8	1.3
<i>Bromus mollis</i>	SG	11.7	1.7			0.1	31.4	0.8	0.7	4.2	0.1	1.1	2.0	0.1	3.7	2.7	1.8	0.6
<i>Bromus tectorum</i>	SG	1.6					4.9	0.2	6.0	0.1		0.7	0.1		0.5	1.4		0.1
Cirsium arvense	PF						2.1	14.1	17.2	10.4		0.4	0.1					1.1
Convolvulus arvensis	PF	0.2	0.1	0.1	0.7	0.9	2.5	4.6	0.1	0.3		0.4	0.1	0.9		16.2	15.3	0.2
Lathyrus tuberosus	PF																	6.0
Agropyron sp.	PG	11.3	10.8		12.0								13.4			2.0		
<i>Bromus inermis</i>	PG										40.1	27.3	44.2	71.0	27.3	55.3	22.5	16.8
<i>Festuca pseudovina</i>	PG	7.9	40.4	10.5	44.3	84.1	15.7	50.5	18.9	20.3								
<i>Festuca pratensis</i>	PG	0.2		1.3	5.9	0.3												
<i>Festuca rupicola</i>	PG										4.9	8.2	14.0	4.2	51.5	9.6	15.3	34.2
<i>Poa angustifolia</i>	PG	20.2	39.4	86.6	33.9	12.0	4.1	4.1	0.1	1.9	45.8	48.4	24.1	23.6	10.3	2.6	1.2	8.3
Year 3																		
<i>Trifolium striatum</i>	SF											7.8	0.0	1.1				
<i>Vicia hirsuta</i>	SF	0.2		7.8	5.1	17.3		1.2	0.4		1.4	3.4	1.2	4.5		1.3		0.7
Bromus tectorum	SG	6.3			0.1		0.1	0.2	0.5				0.1		1.2	0.3		
Cirsium arvense	PF						10.6	23.6	47.7	22.8		0.5						14.8
Convolvulus arvensis	PF	0.5	0.3		0.5	1.9	4.9	3.0	0.6	0.5		0.1	0.7	1.5		13.5	1.0	0.1
Agropyron sp.	PG	52.9	24.5		7.2								3.4			6.1		
<i>Bromus inermis</i>	PG										15.3	24.9	33.6	46.8	33.1	9.7	29.8	22.6
<i>Festuca pseudovina</i>	PG	16.8	30.3	15.2	47.7	66.3	64.1	58.5	31.3	39.7							0.2	
<i>Festuca pratensis</i>	PG				5.3													
<i>Festuca rupicola</i>	PG										47.0	30.6	14.1	27.3	52.6	60.1	49.9	59.6
<i>Poa angustifolia</i>	PG	18.0	44.7	72.4	31.4	9.3	11.0	12.4	14.2	34.7	29.2	24.4	39.2	16.2	9.4	1.9		16.0

Appendix B. Mean cover proportions of frequent species detected in reference grasslands (species with a mean cover of 5% in at least one grassland were listed). Weeds were indicated with boldface (based on Grime (1979) and Borhidi (1995)). Notations: AR1–3: alkali grasslands, LR1–3: loess grasslands

	FSG	AR1	AR2	AR3	LR1	LR2	LR3
<i>Trifolium campestre</i>	SF	5.4	5.0	1.4			
<i>Vicia hirsuta</i>	SF				10.9	2.9	2.5
<i>Achillea collina</i>	PF	12.9	3.3	14.5			
<i>Achillea setacea</i>	PF		7.5				
Convolvulus arvensis	PF				2.1	7.9	3.7
<i>Galium verum</i>	PF				0.1	5.4	3.5
<i>Lathyrus tuberosus</i>	PF					6.5	2.3
<i>Plantago lanceolata</i>	PF	12.0	9.0	3.8			
<i>Salvia nemorosa</i>	PF				50.0	36.3	20.5
<i>Bromus inermis</i>	PG				32.5	53.8	58.8
<i>Carex praecox</i>	PG				7.3	3.5	0.1
<i>Festuca pseudovina</i>	PG	50.0	65.5	57.5			
<i>Festuca rupicola</i>	PG				3.1	6.3	2.0
<i>Poa angustifolia</i>	PG				2.8	3.7	5.8

Appendix C. Mean seed bank density scores of frequent species and total seed density detected in seed banks of the sown fields (species detected with at least 30 viable seeds total are listed). Weeds were indicated with boldface (based on Grime (1979) and Borhidi (1995)). One seedling recorded in the samples of a certain field corresponds with a seed density of 66 seeds per m²

Species	FSG	AA1	AA2	AA3	AA4	CA1	SA1	SA2	SA3	CA2	AL1	AL2	AL3	AL4	AL5	AL6	SL1	CL1
<i>Amaranthus retroflexus</i>	SF	332	66		464		66			398		133		199		133	464	66
<i>Capsella bursa-pastoris</i>	SF	3647	4708	2719	3183	1326	1724	4841	2785	1459	4377	4974	6234	6963	10,345	5106	464	66
Chenopodium album	SF	2984	597	133	1592	66	1260	597	928	398	199	398	1,525	928	398	4443	5769	133
<i>Conyza canadensis</i>	SF	66	199	663	928			133		531	1194	66	265	66	199	133	66	199
<i>Gypsophila muralis</i>	SF		332	6499	729	133	663	663	531				133	928				
Lamium amplexicaule	SF	199	199			66		729	531	199		531	133		265	66		
<i>Lepidium campestre</i>	SF				2321	464							133	66				
<i>Matricaria chamomilla</i>	SF		1857	1989	199	4642				66							66	
Matricaria inodora	SF	133	597	1260	1857		1326		199	199	332	1260	1260	265	66	199	531	
Polygonum aviculare	SF	1061	729	862	796	66	0	464	531	66	0	133	199	66	995	464		
<i>Spergularia rubra</i>	SF			4642		133					663	0	66	199				
<i>Stellaria media</i>	SF	663	66		1592			332	531		265	862	1459					
Thlaspi arvense	SF	66	332	66	133			3979	398		66	332	1127	265	1724			
Echinochloa crus-galli	SG	0	199	398	66	7029	3913	1592	1459	1326		133	199	199	332		2984	199
Setaria glauca	SG		133	0	0	862	199	6300	3183	1525	1658	3714	3714				66	1260
Setaria viridis	SG							66	133	265		199	663		1790	1525	0	464
Cirsium arvense	PF							1194	66	1790					66			
<i>Epilobium tetragonum</i>	PF	66	796		133	133		66	66	332		66	66	133				199
<i>Typha</i> sp.	PF	2321	2122	597	1194	796	398		265	995	199	265	265	729	265	729	729	1061
<i>Festuca pseudovina</i>	PG	66	133		199		1260	464	66	66								
<i>Poa angustifolia</i>	PG	531	1260	265	199	332	995	398	464	1194	265	265	796		332	133	928	464
Total seed density		14,523	15,120	22,215	16,512	17,043	11,671	12,467	23,741	13,462	9417	13,860	18,833	11,141	18,568	15,053	4775	13,727

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