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Restoring grassland biodiversity: Sowing low-diversity seed mixtures can lead to rapid favourable changes

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A B S T R A C T

We studied the effect of sowing low-diversity seed mixtures (containing 2–3 competitive grass species) on the regeneration of vegetation on croplands previously used as alfalfa fields. In four permanent plots in 10 restored fields (four with alkali and six with loess seed mixture) the cover of flowering plants was recorded and phytomass was measured between 2006 and 2008. We asked three questions: (i) How fast will weedy, short-lived species decrease in abundance during secondary succession enhanced by sowing low-diversity seed mixtures? (ii) Can weeds be suppressed by sowing competitive native grasses, followed up by management by mowing? (iii) Can succession towards the target native grasslands be accelerated by sowing only low-diversity seed mixtures compared to set-aside old field succession? Our results showed that in just two years a vegetation dominated by perennial grasses has developed, which successfully prevented the establishment of weed species. These results suggested that sowing seeds of two or three competitive grass species is an effective tool to eliminate weed domination and to lead towards the restoration of species poor grasslands with grass domination such as alkali grasslands. However, the developed dense perennial grass cover and the accumulated litter may hamper the immigration of specialist species characteristic to reference grasslands. Therefore, the restoration of species-rich grasslands requires the facilitation of the immigration of grassland specialist species by further management (grazing, mowing and/or hay-transport).

1. Introduction

Agricultural intensification and overproduction often leads to the abandonment of croplands in Europe and elsewhere (Ramankutty and Foley, 1999; Cramer et al., 2008). This process has been especially intense in Central and Eastern European countries, where large state-owned or state-run agricultural co-operatives have collapsed and lands were often privatised after 1990. For example, 10% of Hungary's agricultural croplands and pastures have been abandoned recently (Hobbs and Cramer, 2007). The restoration of (semi)natural grasslands on abandoned lands offers a great opportunity to mitigate or stop the processes that damage overall biological diversity (Young, 2000; Ewers and Didham, 2005; Römermann et al., 2005). Although habitat restoration has long been available as a key policy option and conservation tool to preserve or increase biodiversity, it has usually been limited in scope (Walker et al., 2004). One reason why habitat restoration is infrequently applied is that its success cannot be guaranteed because the ecological processes occurring after restoration are often unpredictable. Furthermore, even if restoration is successful, it is not a panacea in itself because post-restoration management is often required to direct ecological processes towards the high-diversity target status (Young, 2000). Therefore, understanding the ecological processes occurring after restoration is essential to design and implement effective conservation actions (Hobbs and Walker, 2007).

The most trivial method to restore grasslands is based on spontaneous processes (old field succession, Prach and Pyšek, 2001). The regeneration of the former grassland vegetation, however, is often slow and highly unpredictable (Hutchings and Booth, 1996). Regeneration is often hindered by the lack of propagules of species of conservation value due to seed bank depletion (Hutchings and Booth, 1996; Thompson et al., 1997; Bissels et al., 2005), lack of nearby propagulum sources or limited dispersal (Simmering et al., 2006; Schmiede et al., 2009), or missing dispersal agents and processes (Strykstra et al., 1997; Ruprecht, 2006). Moreover, regeneration can be hampered by competition from weedy species that often invade abandoned areas (McLendon and Redente, 1992; Prach and Pyšek, 2001). Therefore, more active conservation often attempts to control and accelerate successional changes (Luken, 1991; Pakeman et al., 2002) by sowing propagules

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of species characteristic to the target communities (Pywell et al., 2002; Lepš et al., 2007). Most such studies have applied sowing high-diversity seed mixtures (e.g. 14 species – Warren et al., 2002; 27 species – Jongepierová et al., 2007; 32 species – Foster et al., 2007; 25–41 species – Pywell et al., 2002). However, high-diversity seed mixtures of natural species are often expensive and time-consuming to obtain due to the different times of seed maturation of target species. In few cases, therefore, low-diversity seed mixtures were used, which contain the seeds of a few competitive foundation species only (e.g. 5 species – Manchester et al., 1999; 4 species – Lepš et al., 2007). Although conventional wisdom suggests that high-diversity mixtures are more successful in restoring diverse grasslands over longer time scales, two studies show that seeding with low-diversity mixtures can also lead to diverse grasslands (Manchester et al., 1999; Lepš et al., 2007). Of these two studies, one was conducted at a local scale (total restored area 4 ha, Manchester et al., 1999), and another at a continental scale (similar experiment repeated in five European countries, Lepš et al., 2007). Thus, we do not have information on restoration success at intermediate (e.g. >10 ha) scales. At larger scales, for example, seeding with low-diversity seed mixtures may lead to different successional pathways and more diverse communities, which can increase landscape-level biodiversity.

We studied the early successional changes after grassland restoration on croplands previously used as alfalfa fields. Alfalfa fields are usually not ploughed for 3–4 years, plausibly resulting in a seed bank which is more diverse than that on croplands ploughed more frequently. The restoration of grasslands on alfalfa fields, therefore, either can be more difficult due to the abundance of weeds in the seed bank or can be promising due to the presence of some native species dispersing into the seed bank from adjacent areas. Restoration was conducted with two low-diversity seed mixtures, each containing 2 or 3 competitive grass species for alkali and loess grasslands, respectively, on ten fields scattered in a matrix of marshes and target-state grasslands. We studied the changes in vegetation composition after both methods of restoration and the effects of post-restoration management (mowing) on early secondary succession using permanent plots in a repeated-measures design. We specifically asked three questions: (i) How fast will weedy, short-lived species decrease in abundance during secondary succession enhanced by sowing low-diversity seed mixtures? (ii) Can weeds be suppressed by sowing competitive native grasses, followed up by management by mowing? (iii) Can succession towards the target native grasslands be accelerated by sowing only low-diversity seed mixtures compared to set-aside old-field succession? Our goal was to test these ideas and their potential application in the conservation of grassland biodiversity.

2. Materials and methods

2.1. Site description and history

Our study site was the 'Egyek-Pusztakócsi-mocsarak' marsh and grassland complex (42 km^2), a spatially distinct unit of Hortobágy National Park, a World Heritage Site (East Hungary, N47° 34' E20° 55'). The area has a continental climate with a mean annual temperature of 9.5 °C. The mean annual precipitation is 550 mm; large fluctuations in the mean temperatures and annual rainfall are typical.

According to paleo-ecological studies, the marshland-grassland complex with minimal forest cover in the region has existed at this location since the late Pleistocene (Barczi et al., 2006). Military mapping surveys (1856–66) show the marshland as a floodplain with extensive wetlands separated by arable lands on higher loess plateaus in the 19th century. The region had received regular floods from river Tisza until the 1860s. The lower elevated sites were mostly covered by extensive alkali marshes (*Bolboschoenatalia maritimi* and *Typhaetum latifoliae* and *angustifoliae* Borhidi, 2003). The marshes were surrounded by wet alkali grasslands (*Alopecurion pratensis*). Higher elevations were covered by short dry alkali grasslands (*Festucion pseudovinae*) and loess grasslands (*Festucion rupicolae*). Due to river regulations (1860s) and subsequent drainage attempts, agricultural cultivation has increasingly transformed the landscape, resulting in the fragmentation and degradation of natural habitats. Ploughing and melioration were mainly concentrated to higher elevations covered by loess grasslands and alkali short grasslands. As a result, species-rich dry loess grasslands have remained intact on less than 5% of the area of higher-lying loess plateaus.

The hydrological restoration of the marshes took place between 1976 and 1996, which resulted in the revitalisation and regeneration of the extensive wetlands. The second phase of the landscape-level restoration programme (2004–2008), financed by a LIFE-Nature project, aimed to reduce the areal extent of croplands from 34% to 14% by restoring grasslands on 760 ha of arable land to better approach the conditions of the pre-historic landscape and to eliminate the negative effects of agricultural cultivation (water retention, agricultural pollution from infiltration of fertilizers and pesticides, habitat fragmentation) on the marshes.

2.2. Vegetation of alfalfa fields

Alfalfa fields are typically sown in loess plateaus, characterized by soils with low salt concentrations. One to three-year-old alfalfa fields are species poor, with the cover of alfalfa still exceeding 50–75% in year 3. The most frequent subordinate species are *Capsella bursa-pastoris*, *Matricaria inodora*, *Lolium perenne*, *Taraxacum officinale*, *Bromus mollis*, *B. tectorum*, *Convolvulus arvensis*. Their cover often exceeds 5%. Alfalfa retains a mean cover of 40–50% in five-year-old alfalfa fields and several graminoid species like *Alopecurus pratensis, Elymus hispidus* and *E. repens*, *Poa angustifolia*, and *Festuca pseudovina* or *Festuca rupicola* also appear. After year 3, alfalfa is gradually disappearing but may still show a noticeable cover (e.g. 5–10% in ten-year-old abandoned fields).

2.3. Grasslands targeted by the restoration

The target short alkali dry grassland (*Festucion pseudovinae*) is common in soils with moderate or low salt content in the Hungarian Great Plain. The vegetation is dominated by the grass *F. pseudovina* (40–70% of the total vegetation cover). Subordinate graminoid species and typical herbaceous species are given in Electronic Appendix A.These grasslands are often grazed by cattle or sheep. The heavy grazing and/or degradation are indicated by the presence of ruderal and grazing-tolerant species such as *Cynodon dactylon*, *Gypsophila muralis*, *Hordeum hystrix*, *Plantago lanceolata*, *Lepidium ruderale* and *Polygonum aviculare*.

The target loess grassland (*Festucion rupicolae*) had once been common on loess plateaus and foothills in the Carpathian basin, but most of these grasslands were ploughed in historic times because of the highly productive chernozem soil on which it is formed. The aboveground vegetation is dominated by *F. rupicola*, *F. valesiaca, P. angustifolia, Carex stenophylla*. In several stands *Bromus inermis, Stipa capillata* and *Botriochloa ischaemum* are also dominant. Contrary to the target alkali grasslands, loess grasslands are typically rich in herbaceous species. Characteristic herb species are given in Electronic Appendix B. Several rare and protected species are present in non-degraded, native stands such as *Phlomis tuberosa, Thalictrum minus* and *Ornithogalum pyramidale*. These grasslands were traditionally managed by moderate grazing and/or mowing. Heavily grazed stands are usually species poor with

Table 1
Composition of the sown seed mixtures used during the restoration.

Sown species	Alkali seed mixture (%)	Loess seed mixture (%)
Festuca pseudovina	67	–
Festuca rupicola	–	40
Poa angustifolia	33	30
Bromus inermis	–	30

weedy and grazing-tolerant species (*C. dactylon, Carduus acanthoides, Stachys germanica, Eryngium campestre* and *Cynoglossum officinale*).

2.4. Restoration procedure

Ten alfalfa fields (total 93 ha) were chosen for grassland restoration. Compared to the soil of target communities, the soil of the alfalfa fields was nutrient-rich, especially in phosphorous, due to the previous application of mineral fertilizers. After soil preparation, sowing was conducted using either a loess seed mixture (six fields, 37 ha total) or an alkali seed mixture (four fields, 56 ha). The mixtures consisted of seeds of three or two native grass species. The loess seed mixture contained *F. rupicola*, *P. angustifolia* and *B. inermis*, whereas the alkali seed mixture contained *F. pseudovina* and *P. angustifolia* (Table 1). These species were selected because previous observations suggested that these were foundation species in the target grasslands and potentially strong competitors against weeds. Seeds of the *Festuca* species were harvested in the vicinity of the research area. Seeds of *P. angustifolia* and *B. inermis* were purchased from a commercial source (Mezőgazdasági Kutató-Fejlesztő Kht., Szarvas, Hungary), whose stock had originated from the Hortobágy area. Soil preparation (deep ploughing followed by smoothing by disc harrows) and sowing (25 kg/ha) was conducted in October 2005. The sown fields were mown once per year in the second part of June in 2007 and 2008, and the hay was carried away. No other weed control was applied.

2.5. Sampling design

In each restored field, a 25-m^2 site was chosen randomly (total four sites on alkali and six sites on loess restorations). Within each site, four 1-m^2 permanent plots were selected for study. The percentage covers of vascular plant species were recorded each year (2006–2008) in early June. To obtain a baseline vegetation reference, we also designated sites and permanent plots in nearby natural stands of *Achilleo setaceae-Festucetum pseudovinae* (three sites) and *Salvio nemorosae-Festucetum rupicolae* (three sites) using the same design as described above. The reference stands were sampled in early June 2008. In each sampling period, 10 above-ground phytomass samples per site were collected before mowing, resulting in a total of 100 samples from the restored fields per year. Phytomass samples were dried (65 °C, 24 h), then sorted to litter, graminoid (Poaceae and Cyperaceae) and herbaceous groups. The dry weights of the samples were measured with an accuracy of 0.01 g.

2.6. Data processing and analysis

We classified species into four functional groups: perennial graminoids, perennial herbs, short-lived graminoids, and short-lived herbs. These categories were based on Raunkiaer's life form system; short-lived species group included annuals and biennials, while perennials included geophytes, hemicryptophytes, and chamaephytes. We also calculated the percentage cover based the relative proportions of functional species groups. Temporal changes in cover and species richness were analyzed using one-way repeated-measures ANOVA or Friedman's repeated-measures ANOVA on ranks depending on whether the data met the assumptions of homoscedasticity (evaluated by an *F*-test) and normality (Kolmogorov–Smirnov test). We used Kruskal–Wallis tests to analyse phytomass data that were not from repeated-measures. After significant ANOVAs, we compared groups using the Student–Newman-Keuls procedure (Zar, 1999). We calculated Shannon indices of diversity to characterise vegetation diversity. To explore similarities between restored and reference sites we used Nonmetric Multidimensional Scaling (NMDS) ordination with Bray-Curtis similarity based on percentage cover data (Legendre and Legendre, 1998). We used the metaMDS function of the package "vegan" in R 2.9.0 which provides an NMDS with stable solution from random starts. Species scores were added to the final solution as weighted averages using function wascores (Oksanen et al., 2009). Characteristic (indicator) species of different fields and years were identified by the IndVal procedure (Dufrêne and Legendre, 1997). During the calculations we used 1000 random permutations. The IndVal procedure was calculated by an updated version of the R code published as the electronic appendix of Bakker (2008).

3. Results

3.1. The regeneration process

In year 1 of the study (2006), short-lived weedy herbaceous species dominated the restored fields (*C. bursa-pastoris*, *M. inodora*, *P. aviculare*, *Descurainia sophia, Stellaria media*). Pioneer and weedy short-lived grasses (e.g. annual *Bromus* species: *B. arvensis*, *B. mollis*, *B. sterilis*, and *B. tectorum*) were also detected with considerable cover, especially in the sites sown with alkali seed mixtures. The relative proportion of short-lived species was high in every field in year 1 (Table 2). The short-lived, weedy species have been replaced by perennial graminoids as early as by year 2 (2007) in every site, regardless to the seed mixture sown. In year 2, none of the short-lived species had a cover higher than 5%. The relative proportion and the species richness of short-lived herbs have decreased significantly during the three years of secondary vegetation development, whereas that of perennial grasses increased (Table 2).

The cover of the *Festuca* species sown was typically low in year 1 (most of the sites <5%), but it generally increased thereafter. In contrast, *P. angustifolia* had a cover >5% in six sites already in year 1. From years 1–2, the relative proportion of the grasses sown increased significantly; and by year 3, the cover scores of grasses sown exceeded 50% in all sites (Table 1, Fig. 1). Several unsown perennial grass species (*Elymus repens*, *E. hispidus*, *F. pratensis*) were also established from year 1. A slow immigration of species characteristic to reference grasslands was detected (perennials: *Achillea collina*, *Dianthus pontederae*, short-lived: *Melandrium viscosum*, *Trifolium striatum*, *T. strictum*, *T. angulatum*, *Cruciata pedemontana*). However, their cover was not high even in year 3, when only short-lived vetch species were present with considerable cover (*Vicia hirsuta* and *V. angustifolia*, Electronic Appendices A and B).

3.2. Species richness and phytomass

A total of 95 species were recorded in the plots of the restored fields in the 3 years. Of all detected species, 23 were graminoids, and 72 were herbaceous. Most herbs were short-lived; only 15 perennial species were detected, each of them with low cover. We detected 67 species (15 graminoid, 52 herbaceous) in alkali plots, and 79 species (20 graminoid, 59 herbaceous) in loess plots. Total species richness decreased significantly from years 1 to 2 in both types of restoration (Table 2). From years 2 to 3, a low but

Table 2
Mean proportions and species numbers of important functional groups and average Shannon diversity in the alkali and loess seed mixtures restored fields (mean ± SE, 1-m^2 plots). Significant differences between the years were indicated with different superscript letters (repeated-measures ANOVA or *Friedman repeated-measures ANOVA on ranks, and Student-Neuman-Keuls post hoc test, $p < 0.05$). Data from 1-m^2 plots were pooled on the site level; tests were executed on pooled samples ($n = 6$ in fields seeded with loess mixture, and $n = 4$ in fields seeded with alkali mixture). Each species sown were present in every year in almost every plots surveyed; therefore, species numbers for the sown species are omitted from the table.

	Alkali seed mixture			Loess seed mixture		
	2006	2007	2008	2006	2007	2008
Vegetation relative proportion (%)						
Short-lived herbs	51.3 ± 14.5[a]	10.6 ± 9.1[b]	5.4 ± 2.2[b]	78.6 ± 7.9[a]	3.7 ± 1.6[b]	8.5 ± 3.2[c]
Perennial herbs	0.8 ± 0.8	0.8 ± 0.4	0.6 ± 0.4	0.9 ± 0.7	2.7 ± 2.0	1.9 ± 1.0
Short-lived grasses	11.6 ± 6.0	2.2 ± 1.8	1.5 ± 0.8	3.0 ± 1.5	1.7 ± 0.8	2.7 ± 1.9
Perennial sown grasses	35.3 ± 12.5[a]	71.2 ± 14.6[b]	75.2 ± 7.2[b]	15.9 ± 6.1[a]	86.2 ± 3.0[b]	81.8 ± 4.1[b]
Perennial unsown grasses	1.1 ± 0.5	15.2 ± 4.8	17.2 ± 7.6	1.6 ± 1.4	5.7 ± 3.5	5.1 ± 3.8
Species numbers (m^{-2})						
Total	*17.8 ± 1.8[a]	*9.2 ± 1.6[b]	*7.6 ± 0.9[b]	*17.4 ± 1.8[a]	*7.7 ± 1.2[b]	*9.8 ± 1.1[c]
Short-lived herbs	11.4 ± 1.4	3.0 ± 1.2	2.5 ± 0.6	11.4 ± 1.2	1.7 ± 0.5	3.9 ± 0.7
Perennial herbs	1.0 ± 0.8	1.3 ± 0.5	0.5 ± 0.3	0.9 ± 0.3	1.3 ± 0.9	1.1 ± 0.4
Short-lived grasses	2.5 ± 0.2	0.9 ± 0.6	1.3 ± 0.3	1.6 ± 0.2	1.0 ± 0.4	0.9 ± 0.3
Perennial unsown grasses	0.8 ± 0.4	2.1 ± 0.3	1.4 ± 0.6	0.9 ± 0.4	0.7 ± 0.3	1.0 ± 0.2
Shannon diversity	1.7 ± 0.1[a]	1.0 ± 0.2[b]	1.0 ± 0.1[b]	1.5 ± 0.2	1.2 ± 0.1	1.3 ± 0.1

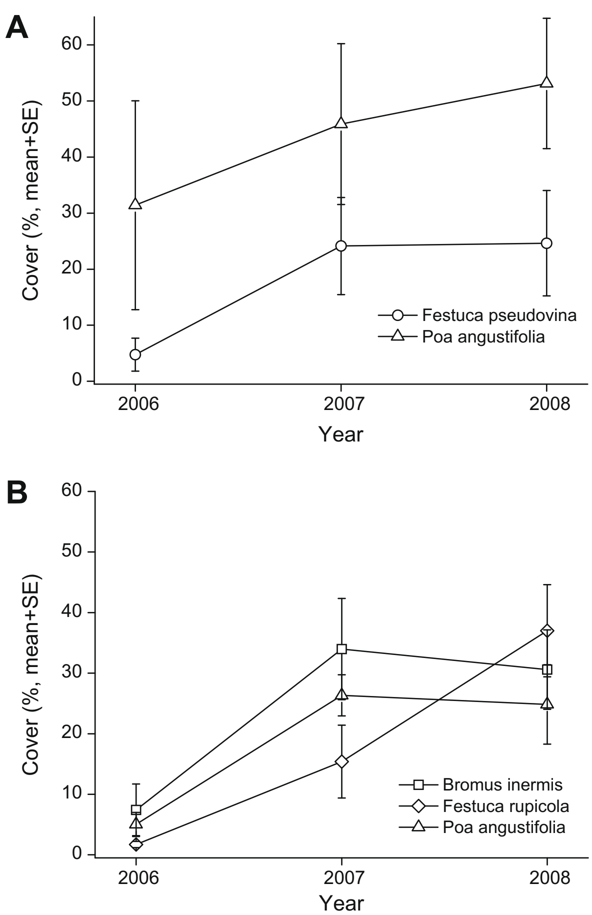

Fig. 1. Changes in percentage cover of sown species between 2006 and 2008 in fields restored using alkali seed mixture (A) and loess seed mixture (B). Data are from six sites restored using loess mixture (pooled samples at site level, $n = 6$) and from four sites restored using alkali mixture (pooled samples at site level, $n = 4$; mean ± SE).

significant increase in species richness occurred in the loess plots, but not in the alkali plots (Table 2). Shannon diversity was highest in year 1 and decreased from years 1 to 2 in both types of restoration. Diversity increased back again from years 2 to 3 in loess plots, but not in alkali plots.

The changes in phytomass were similar in both types of restored fields. Herbaceous phytomass scores were high in all fields in year 1, but decreased by two orders of magnitude by year 2 (to 1–4% of year 1 values). At the same time considerable, seven- to tenfold increase in litter was observed from year 1 to 2 and 3. The phytomass of the grasses sown gradually increased during succession (Table 3).

3.3. Similarity of the restored fields and reference grasslands

The multivariate analysis indicates a clear distinction between alkali and loess plots along the 1st NMDS axis (Fig. 2). There was a continuous shift in the species composition from the weed-dominated stages towards the reference grasslands. The species composition of both plots in years 2 and 3 was more similar to that of reference grasslands than to species composition in year 1. We observed higher similarity between the alkali plots and the reference alkali grasslands than between the loess plots and the loess reference grasslands (Fig. 2). The increasing homogenisation of species composition of various alkali plots corresponded well with the high internal homogeneity of the target alkali grasslands (Fig. 2).

4. Discussion

4.1. Weeds and their suppression

The vegetation in year 1 was dominated by short-lived weedy assemblages, similarly to the findings of other studies (Ruprecht, 2005; Lepš et al., 2007; Török et al., 2008a; Jongepierová et al., 2007). The short-lived weeds, however, were rapidly replaced by perennial species, and already in year 2 the perennial grasses sown typically dominated all fields. Previous studies showed that the success of weed suppression depends on the proportion of grass species in the seed mixture sown. The suppression rate was high only when grass species made up at least 70% of the seed mixture (van der Putten et al., 2000; Warren et al., 2002; Lepš et al., 2007), and it was low when the proportion of grasses was 50% (Stevenson et al., 1995). In the latter cases, high suppression was found for high-density sowing (40 kg/ha, Stevenson et al., 1995).

In all fields, we detected a significant decrease in species richness and diversity already from years 1 to 2. The competitive exclusion of poor competitor, short-lived annuals is one of the possible mechanisms, which can explain the decreasing richness and diversity (Foster and Tilman, 2000; Anderson, 2007). This process

Table 3
Average phytomass of the functional groups on the restored fields (mean ± SE, g/m^2). Significant differences were indicated with different superscripted letters (one-way ANOVA or *Kruskal–Wallis test, $p < 0.05$ both). Data from 20 × 20-cm samples were pooled on the site level; tests were executed on pooled samples ($n = 6$ in fields seeded with loess mixture, and $n = 4$ in fields seeded with alkali mixture).

Phytomass	Alkali seed mixture			Loess seed mixture		
	2006	2007	2008	2006	2007	2008
Herbaceous	*865.6 ± 269.8^{a}	*6.6 ± 2.7^{b}	*11.5 ± 3.6^{b}	*965.5 ± 158.2^{a}	*5.58 ± 4.0^{b}	*41.2 ± 13.7^{c}
Sown grasses	264.2 ± 78.9^{a}	388.8 ± 27.8^{ab}	618.5 ± 97.4^{b}	293.4 ± 69.6^{a}	378.4 ± 49.2^{a}	616.0 ± 66.7^{b}
Unsown grasses	298.4 ± 90.7	109.0 ± 39.0	286.2 ± 127.8	147.2 ± 50.9	36.7 ± 26.9	84.8 ± 59.5
Litter	*28.2 ± 8.5^{a}	*289.7 ± 49.4^{b}	*267.4 ± 36.4^{b}	*37.0 ± 15.9^{a}	*280.3 ± 30.6^{b}	*222.3 ± 51.0^{b}

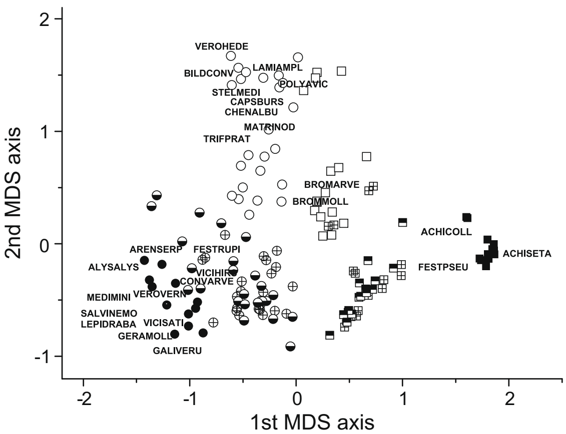

Fig. 2. Similarity between reference grasslands and the restored sites based on the percentage cover of species (Bray–Curtis similarity and NMDS ordination; stress = 21.34). Alkali seed mixture: 2006: □, 2007: ⊞, 2008: ⬒, reference alkali grassland:■. Loess seed mixture: 2006: ○, 2007: ⊕, 2008: ◒, reference loess grassland: ●. Species with IndVal scores higher than 50 were plotted (for species abbreviations, see Electronic Appendix A–B).

is also promoted by high nutrient levels in the soil (Marrs, 1993; Huston, 1979). Our preliminary analyses of soils of the restored fields detected phosphorous and potassium concentrations of several hundred mg/kg (Török et al., 2008b), which most likely had resulted from previous fertilizer use on the restored lands. Mowing in June, timed before the peak flowering time of most weeds, was also likely to reduce the proportion of weeds after year 1. Paradoxically, weed cover might have even been beneficial for the grasses sown because the high cover and mass of weeds probably established a microclimate that facilitated the germination and development of the species sown.

In all restored fields, litter accumulation was observed; at the same time decreasing species richness, mainly the due to the disappearance of weeds, was detected. Only small amounts of accumulated litter of annual herbaceous species were detected in the first year in both types of restored fields (28–38-g/m^2). Litter accumulation of the graminoid species was detected from the second year onwards. The accumulated litter mainly originated from the decay of the secondary sprouting of perennial graminoids, which followed the mowing in June. There was more litter in the restored fields than in regularly mown or grazed alkali and loess grasslands (220–268-g/m^2 in the restored fields and 62–160-g/m^2 in managed alkali and loess grasslands, Török et al., unpublished). The high litter and phytomass production of graminoids in the restored fields were probably caused by the improved nutrient availability following agricultural use. Decreasing amounts of litter were detected from years 2 to 3 in both types of restored fields, which was mainly the result of the regular mowing.

The accumulation of litter possibly changed germination patterns. The accumulated plant litter decreases the irradiance of the soil surface (Stevenson et al., 1995; Diemer et al., 2001), decreases the success of germination (Xiong and Nilsson, 1999; Overbeck et al., 2003) and increases seedling mortality (Tilman, 1993). This effect may also contributed to the rapid decline of weeds, because the pioneer species are more sensitive to litter accumulation than later successional ones (Monk and Gabrielson, 1985; Bartha, 2001).

Parallel to the disappearance of short-lived species, several perennial unsown graminoids became established in the restored fields (*F. pratensis*, *E. hispidus*, *E. repens*). These species frequently occur in alfalfa fields in the region, and after ploughing they could re-establish via vegetative growth, because of their excellent rhizomatous regeneration (van der Putten et al., 2000; Lepš et al., 2007). Furthermore, their germination is not hampered by increased perennial cover and litter (Monk and Gabrielson, 1985).

4.2. Development of perennial grass cover

The theory of "slowing down succession" suggests that the vegetation development slows down after the formation of perennial domination (Inouye et al., 1987; Lepš, 1987; Foster and Tilman, 2000; Török et al., 2008a). Our results are consistent with this theory; the changes in species richness, composition and vegetation cover were significantly lower between years 2 and 3 than in years 1 to 2. However, the time necessary for the changes observed was substantially shorter than could be expected based on previous grassland restorations. Our results support the idea that sowing propagules of late successional species can considerably facilitate the regeneration process (van der Putten et al., 2000; Lepš et al., 2007).

The formation of perennial grass dominance was more rapid than in spontaneous regeneration of old fields reported in other studies. In spontaneously regenerating old-fields on chernozem soil at similar elevations, perennial grass dominance (by *F. rupicola*, *P. angustifolia* and *Koeleria cristata*) was reported only after 10 years (Molnár and Botta-Dukát, 1998). Ruprecht (2005) reported cover values of *F. rupicola* similar to that found here in 10- to 14-year-old spontaneously regenerating old-fields. After heavy goose browsing, the perennial graminoid domination was established spontaneously in bare, nutrient-rich sandy soil only after 4–7 years of secondary succession (*F. pseudovina*, *P. angustifolia* and *C. dactylon*, Török et al., 2008a; Matus et al., 2005). In another sandy old-field study in the Great Plain area in central Hungary, the mean cover of perennials exceeded 50% only after 11–23 years of vegetation development (Csecserits et al., 2007). From abandoned loess plateaus in China, Feng et al. (2007) reported perennial dominance after 6–12 years. Inouye et al. (1987) observed such dominance after 5–15 years of the abandonment of agricultural practice in old fields on Anoka County Sand Plain. Prach and Pyšek (2001) detected perennial grass dominance in the Czech Republic in spontaneously regenerating old fields with various soil types typically after 6–20 years. In our study the speed of the formation of perennial cover was similar to that in other experiments with low-diversity mixtures (Lepš et al., 2007).

The result of NMDS ordination showed that the species composition of restored fields and reference grasslands became progressively more similar (Fig. 2). This tendency was shown both by large changes in life-form composition (decrease of annuals and increase of perennials, see above) and more subtle changes indicated by the appearance of species that are characteristic to the reference grasslands.

4.3. Recruitment of desirable species – implications for restoration

We detected a slow spontaneous immigration of herbaceous species characteristic to reference grasslands. This is in accordance with the findings of other studies of grassland restoration in ex-arable lands (Walker et al., 2004). Most of the reports are sceptic about the spontaneous immigration of the target species. Even where target species were sown in diverse mixtures, only the common generalist species with high competitive ability showed good recruitment (Pywell et al., 2003). A closed and productive vegetation dominated by perennial generalists hampers the chances for the establishment of dispersed species (Walker et al., 2004). Rapid development of perennial cover and litter accumulation proved to be detrimental to species-enrichment and the establishment of target species, due to high competition and the lack of regeneration niches (Critchley et al., 2006; Török et al., 2009). Sowing competitor species was recommended for the sites where noxious weeds were present in high cover or where invasion was likely (Smith et al., 1999; Critchley et al., 2006; Lepš et al., 2007).

Our results suggest that sowing seeds of a few competitive grass species can be a useful conservation tool to restore grasslands and eliminate initial weed domination following the abandonment of agricultural cultivation. Vegetation dominated by perennial grasses, which prevents the long-term establishment of weedy species, developed rather quickly, in 3 years. Even the sowing of low-diversity seed mixtures can quickly lead to semi-natural grasslands when the starting conditions (less disturbed alfalfa fields with adjacent propagulum sources) and management options are carefully matched. Therefore, this method proved to be effective in the restoration of native grasslands dominated by grasses (e.g. alkali grasslands). The full restoration of species-rich grasslands, like loess grasslands, requires facilitating of the immigration of specialist species, for which further management interventions are necessary. Traditional extensive grazing with sheep or cattle can transport propagules of the target species and can enhance their establishment from the natural grasslands to the restored fields (Gibson, 1988; Poschlod et al., 1998). Traditional mowing regimes in the restored fields and the repeated transport of hay from natural grasslands could enhance the proportion of specialists in the restored fields and eliminate the negative effects of limited spontaneous dispersal (Hölzel and Otte, 2003; Donath et al., 2006; Leng et al., 2009).

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Appendices A and B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2009.12.024.

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