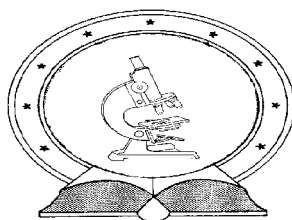# GRASSLAND RECOVERY USING SPONTANEOUS SUCCESSION AND TECHNICAL RECLAMATION: ANALYSIS OF RESTORATION SUCCESS IN SEVERAL GRASSLANDS TYPES

## A SPONTÁN SZUKCESSZIÓ, KASZÁLÁS, ÉS MAGVETÉS SEGÍTSÉGÉVEL TÖRTÉNŐ GYEPREKONSTRUKCIÓ SIKERESSÉGÉNEK VIZSGÁLATA ELTÉRŐ GYEPTÍPUSOKBAN

Egyetemi doktori (PhD) értekezés

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**A doktori értekezés betétlapja**

Ezen értekezést a Debreceni Egyetem Természettudományi Doktori Tanács a **Juhász Nagy Pál Doktori Iskola Kvantitatív és Terresztris Ökológia** programja keretében készítettem a Debreceni Egyetem természettudományi doktori (PhD) fokozatának elnyerése céljából.

Debrecen, 2011.

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Tanúsítom, hogy **Valkó Orsolya** doktorjelölt 2008-2011 között a fent megnevezett Doktori Iskola **Kvantitatív és Terresztris Ökológia** programjának keretében irányításommal végezte munkáját. Az értekezésben foglalt eredményekhez a jelölt önálló alkotó tevékenységével meghatározóan hozzájárult. Az értekezés elfogadását javasolom.

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Értekezés a doktori (Ph.D.) fokozat megszerzése érdekében
a Környezettudomány tudományágban
Írta: **Valkó Orsolya** okleveles Biológus-ökológus

Készült a Debreceni Egyetem **Juhász-Nagy Pál Doktori Iskolája**
(**Kvantitatív és Teresztris Ökológia** programja) keretében

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A doktori szigorlati bizottság:
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# General introduction

Grasslands are vital elements of the historical landscape of Europe and of crucial importance in biodiversity conservation (Nösberger & Rodriguez 1996; WallisDeVries et al. 2002). Grasslands play an important role in the land use of Europe, the 38.1% of all agricultural lands (474.3 million ha) are grasslands (FAOSTAT). Most of the European grasslands are traditionally managed by mowing or grazing which is essential for animal husbandry and support the livelihood of farmers. Traditionally managed seminatural grasslands are of a cultural importance. Grasslands provide important ecosystem services such as recreation, sport and tourism (Isselstein et al. 2005). Grassland biodiversity is a crucial element of the total biodiversity of rural landscapes (Nösberger & Rodriguez 1996). The species richness of plants is very high in many grassland types, both in the form of a high overall richness and a high richness at small spatial scales (Eriksson et al. 2002).

Natural grasslands have been in constant decline in many parts of Europe during the past decades. The area of traditionally managed grasslands reduced by 90% in Sweden (Bernes 1994), by 97% in England (Blackstock et al. 1999) and by 99% in Finland (Vainio et al. 2001). This considerable decline is caused by many factors such as abandonment, afforestation, drainage, conversion into cropland and intensification of management (Poschlod & WallisDeVries 2002). In Western Europe industrialization of the agricultural sector has resulted in considerable changes in land-use patterns and rapidly transformed extent areas to croplands. This is particularly true in countries with improved agriculture such as Great Britain, The Netherlands, Belgium, France and Germany (Kiehl et al. 2010). Seminatural grasslands and their associated species have rapidly declined as a result of intensification. The frequent application of fertilizers (Tilman 1993), substantial nitrogen input from atmospheric deposition (Bakker & Berendse 1999) and commercial seeding (e.g. commercial seed mixtures and/or energie grasses) result in an increased biomass production but decreased species richness (Bakker & Berendse 1999; Pfadenhauer & Grootjans 1999). Wet grasslands were also subject to drainage (melioration) and afforestation by tree plantings (e.g. plantings for biomass production, Hald & Vinther 2000). Export of such intensive agricultural practices to the Eastern and Central European countries of the European Union (EU) can be a major threat to biodiversity in the near future (Pullin et al. 2009). Beyond agriculture, rapid urban development and the exponential growth of linear infrastructures have fragmented the landscape (Pullin et al. 2009). In many regions only small fragments of grasslands have remained, which are isolated by intensively

cultivated agricultural lands and linear infrastructures (Öster et al. 2009). For several species characterstic to grasslands, fragmentation increases the risk of extinction of fragmented populations (Eriksson et al. 2002).

In Central and Eastern Europe in the former socialist era many grasslands were ploughed up, and the use of fertilisers increased. After the collapse of the state-owned agricultural cooperatives the socio-economical changes associated with cheap import and insufficient funds of the new land owners resulted in a large-scale abandonment of croplands (Prach et al. 2007; Pullin et al. 2009). Since 1989 livestock numbers decreased by 50-70% in this region, which had a key impact on seminatural grasslands, large areas of former pastures and hay meadows were abandoned resulting in the loss of grassland biodiversity (Isselstein et al. 2005). The extension of grasslands was decreased by 14.2% in Hungary between 1989 and 2007 caused mainly by abandonment (FAOSTAT 2010).

The projected changes in global climate are likely to affect wetlands and wet grasslands significantly, in their spatial extent, distribution and function (Dawson et al. 2003). Species are expected to track global warming by shifting their distributions towards higher latitudes or higher elevations. Species with restricted ranges, specific habitat requirements, and limited dispersal abilities may be unable to migrate and colonize new areas in a fragmented landscape, thus increasing their extinction risks (Pullin et al. 2009). Changes in precipitation will alter water availability affecting ecosystem productivity with lower summer water availability. Plant species of wetlands and wet grasslands are particularly vulnerable to climate change because of the delicate balance between the rainfall, temperature and evapotranspiration that governs their physiology (Dawson et al. 2003).

The restoration of seminatural grasslands is a top priority of nature conservation activities in Europe since the 1970s (e.g. Bakker 1989; Walker et al. 2004). There is an increasing social awareness to maintain and enhance grassland biodiversity which resulted in the establishment of agri-environmental schemes (Isselstein et al. 2005). Nowadays approximately 20% of the agriculturally used area in the European Union is managed under agri-environmental schemes (Rounsewell et al. 2005). Many LIFE Nature programs funded by the European Commission are concerned with grassland restoration. A search of a database that contains information on projects between 1992 and 2009 under the LIFE-program (http://ec.europa.eu/environment/life/ project/Projects/index.cfm), using the word 'restoration' and filtering to 'natural and seminatural grassland formations' returns 290 projects (Török et al. 2011a).

Grassland restoration is generally applied to (i) recover former biodiversity, (ii) establish novel grasslands and increase the area of grassland fragments, (iii) create connections between and buffer zones around grassland fragments, thereby negative influences from surrounding agricultural areas (infiltration/runoff of

chemicals, disturbance etc.) can be reduced (Critchley et al. 2003; Karlík & Poschlod 2009). Several grassland restoration techniques are used depending on the type of human disturbance and level of degradation of the subjected area. If basic grassland vegetation is still present but former management altered and the grassland is impoverished or abandoned, the major aim is to recover its former species richness by restoration. One of the most frequently applied restoration methods is to resume the traditional management (e.g. mowing or low levels of grazing). Some techniques are used to decrease nutrient availability by topsoil removal or restore former hydrological state of the area e.g. by rewetting (Kiehl et al. 2010). Many cases, such measures alone are not sufficient to re-establish target communities without active introduction of target grassland species (Bakker & Berendse 1999; Walker et al. 2004). Target species, e.g. several characteristic grassland specialists, often have limited dispersal patterns and transient seed banks (Bakker et al. 1996; Bossuyt & Honnay 2008; Valkó et al. 2011). Only few target species build up long-term persistent seed banks (Thompson et al. 1997) and their seed bank is often destroyed during a long-term agricultural use (Bakker et al. 1996; Bekker et al. 1997). In this case the increase of species richness is only possible by direct reintroduction of species either by seed sowing, hay or topsoil transfer or planting of individuals (Török et al. 2011a).

Grassland restoration on abandoned cropland is one of the most frequently used habitat restoration actions in Europe (Hobbs & Cramer 2007). In contrast with agricultural intensification, large-scale abandonment of low-productivity croplands is common in certain parts of Europe and the world (Cramer et al. 2008; Török et al. 2011a). For example, 10% of all croplands (600,000 hectares) were abandoned in Hungary between 1990 and 2004, and the rate of abandonment was similar (10-20%) in four other Central and Eastern European countries (Hobbs & Cramer 2007). Thus, the restoration of grasslands on former croplands offers a great opportunity to mitigate or halt the processes that threaten grassland biodiversity (Stevenson et al. 1995; Török et al. 2011a). The most frequently applied methods of grassland restoration are spontaneous succession and sowing seed mixtures, which will be discussed below. Other possibilities are hay transfer (Kiehl et al. 2006; Donath et al. 2007), topsoil removal or transfer (Aldrich 2002; Pywell et al. 2002) and planting of plant individuals (Kirmer & Tischew 2006; Du et al. 2007) which are less frequently applied in Hungary both in agriculture and grassland restoration. Selection of the proper methodology regarding its cost efficiency, the required manpower and agricultural machinery and the targeted grassland is a key issue in grassland restoration.

The least expensive way of grassland restoration is spontaneous grassland recovery based on *spontaneous succession* (old-field succession, Prach & Hobbs

2008). This method is applied worldwide and warranted promising at smaller croplands where propagule sources are available in the adjacent natural vegetation (Ruprecht 2006; Prach & Řehounková 2008; Vida et al. 2008). In fragmented landscapes with low availability of propagules of target species and dispersing agents, the spontaneous recovery of grasslands is often slow or hindered (Manchester et al. 1999; Matus et al. 2003a; Simmering et al. 2006; Foster et al. 2007). Succession can stop in an early stage due to the increased dominance of noxious competitors (Prach & Pyšek 2001). Grassland restoration by spontaneous succession can be slow or unpredictable in several cases, thus, it is often necessary to direct vegetation changes with more active restoration measures (Török et al. 2011a).

   *Sowing seeds* of characteristic species of the target community is a widely used restoration method in conservation practice (Hedberg & Kotowski 2010; Kiehl et al. 2010; Rydgren et al. 2011; Török et al. 2011a). The composition of a seed mixture depends generally on (i) the targeted vegetation, (ii) the extension of the former cropland, (iii) the budget and manpower background of planned restoration, and (iv) the availability of seed sources of target species. Low-diversity seed mixtures typically contain seeds of 2-8 species, which are usually the dominant species of the target vegetation, while high-diversity seed mixtures usually contain seeds of more than 10 species (Kiehl et al. 2010; Török et al. 2011a). The seeds for restoration can be purchased from commercial sources or collected by local harvesting. It is advisable to use seeds sourced local provenance (van der Mijnsbrugge et al. 2010) as local ecotypes are better adapted to the local environmental conditions (Aldrich 2002). Low diversity seed mixtures can be effective in the restoration of basic grassland vegetation dominated by perennial grasses as fast as in several years (van der Putten et al. 2000; Lepš et al. 2007; Vida et al. 2010). However the immigration of rare target species can be very slow, so restoration of diverse grasslands can last much longer than basic grassland vegetation (Walker et al. 2004). Sowing high diversity seed mixtures in small patches (to establish potential sources of colonizing propagules) within a larger area sown with low diversity seed mixture can be a solution to this problem (Török et al. 2011a). For the total recovery of species-rich vegetation further post-restoration management (e.g. mowing, grazing, overseeding or hay transfer) is often needed (Deák & Kapocsi 2010).

   There is an urgent need for evidence based and well documented restoration projects to provide useful information for conservation practitioners and site managers (Sutherland et al. 2004). Designed case studies are necessary to evaluate the success of each method used for grassland restoration (e.g. Török et al. 2011a).

# Aims of the study

The present Ph.D. dissertation contains four chapters altogether. Each chapter is based on results published as an impacted paper of the author. The four chapters concern with different aspects of grassland restoration as follows:

*Chapter 1*: We studied mown and abandoned stands of acidic fen- and dry-mesophilous hay making meadows to evaluate the potential role of soil seed banks in the recovery of these grassland types. The following questions were asked: (i) To what extent is aboveground vegetation represented in the seed banks of different meadow types? (ii) Do the soil seed banks contain species that are not represented in the above-ground vegetation? (iii) What is the size of the seed bank for restoration target species? (iv) Do the density and species richness of the seed banks differ between mown and abandoned stands within the same meadow type? (v) Does management status or vegetation type have more of an effect on seed bank richness and density?

*Chapter 2*: The overall aim of this study was to examine the role of spontaneous succession in the restoration of loess grasslands in former lucerne fields as a cost-effective strategy for grassland recovery. We studied the spontaneous regeneration of loess grasslands in extensively managed lucerne fields using space for time substitution, addressing the following questions: (i) How effective is lucerne in weed control? (ii) How quickly does lucerne disappear? (iii) How fast does grassland recover in extensively managed lucerne fields?

*Chapter 3*: We evaluated the use of low diversity seed mixtures recovering basic loess and alkali grassland vegetation. We sowed two types of low-diversity seed mixtures on croplands formerly used as lucerne fields. We asked three questions: (i) Can weeds be suppressed by sowing competitive native grasses, followed up by management by mowing? (ii) How fast does the cover of sown grasses develop after sowing low diversity seed mixtures? (iii) Can succession towards the target grasslands be accelerated by sowing only low-diversity seed mixtures compared to set-aside old-field succession?

*Chapter 4*: We studied the role of litter accumulation in weed suppression and early vegetation dynamics in grassland restoration using the sowing of low diversity seed mixtures on former lucerne fields. The following study questions were selected: (i) What is the effect of the accumulating phytomass of graminoids and litter on the phytomass of early colonisers? (ii) Are the amount of graminoid phytomass and litter higher, and the heterogeneity of these scores lower in sown fields than in natural grasslands? (iii) Is the amount of forbs lower in restored fields than in target grasslands?

# Materials and methods

## Study sites

### *Gyertyán-kút meadows (Chapter 1)*

The study site, called "Gyertyán-kúti-rétek", is located in the Zemplén Mountains between the villages of Telkibánya and Regéc (NE Hungary; 48°26.1-26.7' N; 21°21.6-22.3' E) on a plateau with a height of 640-720-m a.s.l. It is surrounded by oak (*Quercus petraea*), oak-hornbeam (*Qu. petraea* and *Carpinus betulus*) and mountain beech (*Fagus sylvatica*) forests. The bedrock is amphibol-rich andesite on which podzolic brown forest soils with heavy, clayey, humus-rich and acidic topsoils were formed. Mean annual temperature of the site is about 7.5–8.0ºC whereas mean annual precipitation is 750-800-mm with a midsummer maximum. The meadows were established in the 18th century; their area measured approximately 100 hectares in the past. They were managed by mowing with scythe then removing the hay by hand raking once a year, in July. Traditional management created and maintained highly species-rich vegetation which harboured over 350 vascular species, including over 40 legally protected ones. Management has gradually been abandoned since the 1960s, resulting in the colonization of wind-dispersed tree species (mostly *Betula pendula* and *Carpinus betulus*). Large stands of young birch forests were cut and traditional management was gradually resumed since 1985 (Simon et al. 2007).

Stands of the two most widespread acidic meadow types, fen meadows and dry-mesophilous meadows were studied. Fen meadows (*Junco-Molinion*) are located in lower elevations and on humus rich soils. They are dominated by *Molinia arundinacea*. Dry-mesophilous meadows (*Cirsio pannonicae-Brachypodion pinnati*) are located in higher elevations with drier and on less fertile soils. Typical graminoids in these meadows include *Brachypodium pinnatum*, *Calamagrostis arundinacea* and *Carex montana* (Borhidi 2003).

### *Extensively managed lucerne fields in Hortobágy region (Chapter 2)*

The study area is located in the Hortobágy Puszta (Hortobágy National Park), in East-Hungary. Hortobágy Puszta with an area of 85,000 ha is one of the large grassland ecosystems in Europe, with vegetation characteristic of alkali and loess grasslands. The climate is moderately continental with a mean annual

temperature of 9.5°C. Mean annual precipitation is about 550 mm. The yearly maximum precipitation falls in June (mean 80 mm) with high year-to-year fluctuations (Molnár 2004). Historically, loess grassland vegetation (*Festucion rupicolae*) covered the highest elevations in the region (Borhidi 2003). At lower elevations, loess grasslands were surrounded by dry alkali short grasslands (*Festucion pseudovinae*), alkali wet meadow (*Alopecurion pratensis*) and alkali marsh vegetation (*Bolboschoenatalia maritimi*) (for more details see Molnár et al. 2008; Molnár & Borhidi 2003). The loess grasslands have been ploughed up in the last centuries and many of the remaining grassland fragments are degraded by moderate or heavy grazing by cattle and/or sheep. The most degraded loess pastures (*Cynodonti-Poëtum angustifoliae*) are characterised by a high cover of grazing tolerant graminoids (*Cynodon dactylon*, *Poa angustifolia*, *Festuca pseudovina*, *F. rupicola* and *Carex stenophylla*) and forbs (*Galium verum*, *Euphorbia cyparissias*, *Cruciata pedemontana*, *Myosotis stricta*, *Achillea collina* and *Convolvulus arvensis*). At heavily grazed sites, thistles dominate (*Carduus acanthoides*, *Cirsium arvense*, *Ononis spinosa*, *Eryngium campestre*). Only small patches of less degraded loess steppe grasslands (*Salvio nemorosae-Festucetum rupicolae*) have remained. The characteristic graminoids for these grasslands are *Festuca rupicola*, *Bromus inermis*, *Koeleria cristata*, *Stipa capillata*, *Alopecurus pratensis* and *Poa angustifolia.* They are rich in perennial forb species, and harbour several characteristic loess specialists (*Salvia nemorosa*, *Salvia austriaca*, *Phlomis tuberosa*, *Thalictrum minus*, *Thymus glabrescens*).

In the study region lucerne or alfalfa *Medicago sativa* is sown after deep ploughing at the high elevations formerly covered by loess grasslands. Seed sowing density is typically 30 kg/ha. There are intensively and extensively managed lucerne fields. Intensive management means regular mowing associated with the application of fertilisers and pesticides. After three years intensively managed fields are re-sown or shallow disked. Extensive management means only regular mowing twice a year. Every year 10-50 hectares intensively managed lucerne fields were replaced by extensively managed ones in the Hortobágy National Park. The vegetation of 1, 3, 5 and 10-year-old extensively managed lucerne fields (three fields in each age group) was monitored in 2009. The study fields were situated on loess plateaus between 87-94 m a.s.l., within a 25 km radius, in the vicinity of Egyek, Tiszacsege, Karcag and Nádudvar (N 47°26'; E 21°01'). None of the study fields were directly connected to loess grasslands, which was the most common vegetation at this elevation in the region (Török et al. 2010). The fields were mown twice a year but no further management was applied. Small patches of loess grasslands and, at lower elevations, alkali marshes, alkali wet meadows and alkali short grasslands were present in proximity to most of the fields.

*Grassland restoration fields in Egyek-Pusztakócs region (Chapters 3-4)*

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 (Molnár 2004).

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. 2003). Military mapping surveys (1856-66) show the marshland as a floodplain with extensive wetlands separated by croplands 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 short alkali grasslands. As a result, species-rich dry loess grasslands have remained intact on less than 5% of the area of higher elevated 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 (Lengyel et al. 2007). The second phase of the landscape-level restoration programme (2004-2008), financed by a LIFE-Nature project, aimed at to reduce the areal extent of croplands from 34% to 14% by restoring grasslands on 760 ha of former croplands in order to get closer to 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. Grasslands targeted by the restoration were short alkali dry grasslands (*Festucion pseudovinae*) in the lower and loess grasslands (*Festucion rupicolae*) in the higher elevated sites.

Ten former lucerne fields (total 81 ha) were chosen for grassland restoration. Compared to the soil of target communities, the soil of the restored fields was nutrient-rich, especially in phosphorous, due to the previous application of mineral fertilizers. Sowing was conducted using either a loess seed mixture (six fields, 23 ha

total) or an alkali seed mixture (four fields, 58 ha total). The mixtures consisted of seeds of three or two native grass species. The loess seed mixture contained *Festuca rupicola*, *Poa angustifolia* and *Bromus inermis*, whereas the alkali seed mixture contained *Festuca pseudovina* and *Poa angustifolia*. 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 and the hay was carried away. No other weed control was applied.

## Sampling design

### Vegetation and phytomass sampling

In Gyertyán-kút meadows (Chapter 1), four stands (each abandoned in the late 1960s) from the two meadow types, were studied. In two mown stands traditional management was resumed in 1993 while two abandoned stands were left unmanaged. In each stand aboveground vegetation was recorded in five 2×2-m sized permanent plots in July 2004. A species list was compiled for each plot and the number of flowering shoots was recorded.

In extensively managed lucerne fields (Chapter 2), three 25-m$^2$ sample sites were chosen randomly. Within each site, the percentage cover of vascular plants was recorded in four 1-m$^2$ plots in early June 2009, before the first mowing. We recorded the vegetation of three variously degraded stands of loess grasslands (*Festucion rupicolae*) for baseline vegetation reference: 1) a formerly heavily grazed *Cynodonti-Poëtum* stand, 2) a species-rich loess balk stand with *Bromus inermis* dominance, and 3) a regularly mown species rich stand of *Salvio nemorosae-Festucetum rupicolae* grassland. We used the same sampling design as in extensively managed lucerne fields.

In Egyek-Pusztakócs, in each restored field, a 25-m$^2$ site was chosen randomly. Within each site, four 1-m$^2$ permanent plots were selected for study. The percentage covers of vascular plant species were recorded in the first three years after sowing (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*

with *Bromus inermis* dominance (three sites) using the same design as described above. The reference stands were sampled in early June 2008.

In extensively managed lucerne fields and restored fields, ten 20x20-cm sized aboveground phytomass samples per site were collected before mowing in each sampling period. Phytomass samples were dried (65 $^{\circ}$C, 24 hours), then sorted to litter, graminoids (Poaceae and Cyperaceae) and forbs (dicots and non-graminoid monocots). The species lists of forbs were recorded. The phytomass of lucerne was hand sorted. Dry weights were measured with an accuracy of 0.01 g.

*Seed bank sampling*

Soil seed banks were studied in Gyertyán-kút meadow swith the seedling emergence method. Six soil cores (4-cm in diameter and 10-cm in depth) per plot were drilled after snowmelt in 2005 (fen meadows) and in 2006 (dry-mesophilous meadows). Two vertical segments (0-5-cm, 5-10-cm) were separated; then identical segments from the same plot were pooled. This sampling design enabled the detection of a species with a 95% probability, provided it had at least 80 seeds/m$^2$ and a non-aggregated seed bank (Thompson et al. 1997). Sample concentration was used to reduce sample volume and to promote germination (ter Heerdt et al. 1996). Vegetative organs were retained 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 maximum of 3-4-mm thick layer on trays, previously filled with 5-cm of steam-sterilized potting soil. Trays were illuminated with natural light in a greenhouse shaded by Rachel nets from May to August. Seedlings were regularly counted, identified then removed. Unidentified specimens were transplanted then grown until identified. In early July, when no seedlings emerged, regular watering was stopped, dried sample layers were crumbled and turned. In early September, watering was re-started and continued until late October. Occasional seed contamination (e.g. dispersal by wind) was monitored in sample-free control trays filled with steam-sterilized potting soil.

## Data processing

In the study for seed banks of hay meadows, species were grouped into 'graminoids' i.e. Poaceae, Cyperaceae and Juncaceae and 'forbs', i.e. dicots and non-graminoid monocots (including Liliaceae, Typhaceae, Iridaceae and Orchidaceae). Non-woody stress tolerant species characteristic to the studied meadow types (according to Grime 1979, Borhidi 1995), including legally protected ones were considered as target species. Seedlings of *Juncus conglomeratus* and *J.*

*effusus* were pooled because of identification difficulties. The vast majority (ca. 90%) of their transplants proved to be *J. conglomeratus*. Greenhouse weeds and wind-dispersed pioneers detected in control trays were excluded from analyses. Seedlings that died before being identified (0.3% of totally emerged seedlings) were also excluded. Species were classified into seed bank type categories based on Thompson et al. (1997) using vegetation records and vertical distribution data of the seed bank (density records for the 0-5 and 5-10-cm layer, respectively). The proportion of species with a persistent seed bank type was then calculated. Species with low frequency in the established vegetation (detected in a maximum of three plots from a total of twenty within a meadow type) and with low seed numbers (less than three viable seeds detected in a meadow type) were not classified into seed bank types; thus they were excluded from persistency calculations. Accidentally occurring ferns (forming no seeds) and orchids (with generally acknowledged cultivation difficulties; Thompson et al 1997) were similarly excluded. The effects of management and meadow type on important vegetation and seed bank variables were analyzed using two-way ANOVA; these variables were ln(x+1) transformed prior to statistical analyses. The mean numbers of flowering shoots and seed densities of frequent species were compared with t-test on ln(x+1) transformed data, between mown and abandoned meadow stands (Zar 1999). Species were considered frequent when they had more than 50 flowering shoots in the vegetation, and/or at least 50 viable seeds detected in the seed bank of at least one meadow type. Vegetation and seed bank composition were compared between mown and abandoned stands of the two meadow types with Sørensen similarity using MDS ordination (Legendre & Legendre 1998). Correlations between the number of flowering species in the vegetation and the species richness in the seed banks, as well as the correlation for the number of flowering forbs and the number of forb species in seed banks were analyzed by Spearman rank-correlation.

In studies performed in extensively managed lucerne fields and in restored fields, we classified the species into four functional groups using life-form (based on Raunkiaer's life form system, Raunkiaer 1934) and morphological categories (graminoids and forbs). These were perennial graminoids, perennial forbs, short-lived graminoids, and short-lived forbs. Annuals and biennials are short-lived, and geophytes, hemikryptophytes, and chamaephytes are perennials. In Chapters 2 and 4, the functional group of the weeds was classified using Grime C-S-R strategy types (Grime 1979) which was modified and adapted to local conditions by Borhidi (1995). The species groups AC (adventive competitors, e.g. *Conyza canadensis*, *Ambrosia artemisiifolia*), RC (ruderal competitors, e.g. *Cirsium arvense*, *Elymus repens*) and W (weeds, mostly annual and biennial weedy grasses and forbs) were considered as weeds. We calculated the percentage cover based on the relative

proportions of functional species groups.  In Chapter 2, the cover, species richness and phytomass data of the differently aged extensively managed lucerne fields were compared using General Linear Mixed-Effect Models (GLMM) and Tukey test (Zuur et al. 2009). Field age (time) was included as a fixed effect and field/block structure as a random effect. To analyse correlations between the different phytomass groups and sites we used DCA ordination, with square root transformed datasets. DCA was calculated by CANOCO 4.5 (ter Braak & Šmilauer 2002).

We used cover based Shannon diversity to characterise vegetation diversity, and Sørensen dissimilarity for vegetation changes. Characteristic (indicator) species of differently aged lucerne fields and reference grasslands and of different restored fields and years were identified by the IndVal procedure (Dufrêne & Legendre 1997); during the calculations 10,000 random permutations were used. The IndVal procedure was executed by a revised version of the R code published as the electronic appendix of Bakker (2008). 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 & 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).

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). The mean values of phytomass were compared using repeated-measures ANOVA on datasets pooled at the field level. We used the Tukey test to identify significantly different groups ($p<0.05$) (Zar 1999). The differences of phytomass between alkali and loess seed mixtures sown fields and reference grasslands were analysed using one-way ANOVA and Tukey test ($N$=10 for each field; datasets of alkali seed mixture sown fields and alkali grasslands were separately tested from loess seed mixtures sown fields and loess grasslands). In Chapter 3, 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). In Chapter 4, we calculated the heterogeneity of graminoid phytomass and litter using the Gini-coefficient (Zar 1999). Correlation between the litter, graminoid phytomass, and phytomass and species richness of weedy forbs were calculated by Spearman's rank-correlation (Zar 1999). Tests were executed using SigmaStat 3.1 (basic statistics), R (ANOVA, Gini-coefficient, Spearman correlation, R-Development Core Team 2010).

# Chapter 1

# Restoration potential in acidic dry-mesophilous and fen meadows

## Introduction

Extensively managed hay meadows in mountain regions of Europe were originally created by forest cutting and maintained extensively by low intensity mowing (Fischer & Wipf 2002; Zeiter et al. 2006). Due to the changes in agro-environmental schemes in the last few decades an increased abandonment of these meadows was reported from many regions in Central-Europe (Stampfli & Zeiter 1999; Diemer et al. 2001; Poschlod et al. 2005). The mountain hay meadows are among the most species rich communities in Europe and harbour many threatened plant and animal species (Losvik 1999; Stampfli & Zeiter 1999; Ilmarinen et al. 2009). They are therefore considered to be habitats of outstanding conservational value (Dietschi et al. 2007). Restoration of former biodiversity and conservation of the remaining, often fragmented meadow stands, are high priorities from a nature conservation perspective (Smith et al. 2002).

The abandonment of hay meadows is often followed by declining species richness (Bekker et al. 1997; Stampfli & Zeiter 1999; Stammel et al. 2006). Litter accumulation following cessation of management leads to an increasing dominance of a few competitive graminoids and often results in the disappearance of most subordinate forbs due to increased shading (Billeter et al. 2007; Rudmann-Maurer et al. 2008). Still there are open questions regarding the success of restoration of species richness; e.g. are there any target species already missing from aboveground vegetation of abandoned stands still present in the soil seed banks, and how does their persistence vary in different grassland types with similar history and management?

There are contrasting views on the possible role of soil seed banks in grassland restoration. Several studies emphasize that soil seed banks form an important source for re-colonization (Bakker & Berendse 1999), particularly when species dispersal is limited (Rosenthal 2006; Simmering et al. 2006). However, other investigations have 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. Under-

representation of target species in databases may hamper the understanding of the seed banks' role in community regeneration (Thompson et al. 1997; Csontos 2001).

*Aims of the study*

To address some of these issues we studied mown and abandoned stands of acidic fen- and dry-mesophilous meadows with the aim of evaluating the following questions: (i) What proportion of total species richness is represented in the seed banks of different meadow types? (ii) Do the seed banks contain species that are not represented in the above-ground vegetation? (iii) What is the size of the seed bank for restoration target species? (iv) Does the density and species richness of the seed banks differ between mown and abandoned stands within the same meadow type? (v) Does management status or vegetation type have more of an effect on seed bank richness and density?

## Results

*Vegetation*

In total, 158 species (32 graminoids and 126 forbs) were recorded in the study plots. A larger diversity of forbs was detected in dry-mesophilous meadows (100 forb species, 79% of total forbs) than in fen meadows (80 species, 63% of total forbs). The species richness of graminoids was approximately the same in both meadow types (25 and 26 species, respectively). The studied meadow types shared 73 species; these species displayed different frequencies and levels of flowering success in the two meadow types. In both meadow types species richness, richness of forb species and flowering shoots of forbs proved to be significantly higher in mown stands than in abandoned ones. Higher mean scores of total and of forb species richness were detected in the dry-mesophilous meadows than in the fen meadows (Appendix 1.1). Mowing had a positive effect on all the studied vegetation characteristics in both meadow types (Table 1.1).

Out of the 24 frequent flowering species in fen meadows six had significantly higher flowering success in mown stands (*Briza media* $t$=2.473, p=0.024, $n$=10; *Festuca ovina* $t$=5.648, $p$<0.001, $n$=10; *Luzula multiflora* $t$=2.762, $p$=0.013, $n$=10; *Plantago lanceolata* $t$=3.904, $p$<0.001, $n$=10; *Thymus pulegioides* $t$=3.904, $p$=0.001, $n$=10; and *Viola canina* $t$=5.515, $p$<0.001, $n$=10). In abandoned stands only *Molinia arundinacea* ($t$=4.367, $p$<0.001, $n$=10) reached significantly higher flowering success. In dry-mesophilous meadows, 4 out of the 14 frequent flowering species had a significantly higher number of flowering shoots in mown

plots (*Helianthemum ovatum* $t$=3.476, $p$=0.003, $n$=10, *Thesium linophyllon* $t$=2.511, $p$=0.022, $n$=10, *Thymus pulegioides* $t$=2.853, $p$=0.011, $n$=10, and *Veronica officinalis* $t$=3.711, $p$=0.002, $n$=10). Only *Calamagrostis arundinacea* ($t$=5.776, $p$<0.001, $n$=10) had significantly higher mean numbers of flowering shoots in abandoned than in mown dry-mesophilous meadow stands.

**Table 1.1.** Two way ANOVA of the vegetation and seed bank characteristics of the meadows ($n$=10). Significant effects ($p$<0.05) are denoted by boldface.

| | Meadow type | | | Management | | | Type × Management | | |
|---|---|---|---|---|---|---|---|---|---|
| | $F_{1,36}$ | MS | $p$ | $F_{1,36}$ | MS | $p$ | $F_{1,36}$ | MS | $p$ |
| **Vegetation** | | | | | | | | | |
| Species richness | 8.702 | 0.324 | **0.006** | 19.362 | 0.720 | **<0.001** | 0.045 | 0.002 | 0.834 |
| Forb species richness | 18.776 | 0.631 | **<0.001** | 14.153 | 0.475 | **<0.001** | 0.470 | 0.016 | 0.497 |
| Flowering species richness | 2.310 | 0.321 | 0.137 | 7.225 | 1.003 | **0.011** | 2.115 | 0.294 | 0.155 |
| Flowering forb species richness | 2.385 | 0.386 | 0.131 | 4.286 | 0.694 | **0.046** | 1.410 | 0.228 | 0.243 |
| Number of flowering shoots of forbs | 1.105 | 0.627 | 0.300 | 13.370 | 7.588 | **<0.001** | 0.154 | 0.087 | 0.697 |
| **Seed bank** | | | | | | | | | |
| Species richness | 34.735 | 1.825 | **<0.001** | 0.008 | 0.001 | 0.931 | 0.198 | 0.010 | 0.659 |
| Forb species richness | 21.031 | 1.867 | **<0.001** | 0.106 | 0.009 | 0.746 | 2.004 | 0.178 | 0.166 |
| Number of seedlings | 861.011 | 72.784 | **<0.001** | 0.615 | 0.052 | 0.438 | 3.406 | 0.288 | 0.073 |
| Number of seedlings excluding *Juncus* | 138.739 | 10.979 | **<0.001** | 0.492 | 0.039 | 0.488 | 5.713 | 0.452 | **0.022** |
| Number of forb seedlings | 71.828 | 12.216 | **<0.001** | 0.023 | 0.004 | 0.881 | 6.382 | 1.085 | **0.016** |

*Seed banks*

Altogether 94 species (38 graminoids and 56 forbs) were found in soil samples. In fen meadows 44% of aboveground species possessed any seed banks whereas in dry-mesophilous meadows the same figure was 26%. These proportions for target species were 44% and 29%, respectively, while the proportion of target species detected only in seed banks was 11% in both meadow types. Out of the 31 species detected in soil seed banks of both meadow types, only two species (*L. multiflora* and *Campanula patula*) were similarly frequent. Samples from different meadow types proved to be similarly rich in species, but a lower number of forbs was detected in the seed banks of dry-mesophilous meadows compared to fen meadows. Mean seed densities were about ten to twenty times higher in fen meadows than in dry-mesophilous ones (Appendix 1.1). Total seed densities excluding the dominant *Juncus* species, and the seed density of forbs were also two to four times higher in fen meadows, than these scores in the dry-mesophilous meadows (Appendix 1.1). All studied seed bank characteristics were significantly affected by the meadow type. No overall effect of management on the seed banks

was revealed on the density of persistent seed banks (Table 1.1). In fen meadows *M. arundinacea* had much higher densities in the abandoned plots ($t=9.709$, $p<0.001$, $n=10$), whereas *Agrostis canina* ($t=4.041$, $p<0.001$, $n=10$) and *Lychnis flos-cuculi* ($t=3.920$, $p=0.001$, $n=10$) possessed more dense seed banks in the mown stands. None of the detected species had significantly different seed densities in differently managed dry-mesophilous meadow stands.

*Similarity of above and belowground samples*

The MDS ordination showed a clear distinction between vegetation and seed banks (Fig. 1.1). Similarities between vegetation and seed banks differed greatly according to the vegetation type (Sørensen similarities for fen meadows: 0.41 to 0.53, whereas for dry-mesophilous meadows 0.28 to 0.36). Based on specific vegetation and seed bank data we were able to classify seed longevity of 84 species in fen- and 88 species in dry-mesophilous meadows, respectively. Persistent records in fen meadows comprised 49% of all classified species and 33% in dry-mesophilous meadows. In fen meadows a strong positive correlation was revealed between the number of flowering species in the vegetation and the species richness in the seed banks (Spearman rank correlation; $p<0.001$, $n = 20$, $r = 0.68$) and the same holds for the forbs ($p<0.001$, $n = 20$, $r = 0.70$). No such correlations were found in dry-mesophilous meadows.

In fen meadows almost all frequent graminoids of the vegetation had a considerable number of viable seeds, whereas in dry-mesophilous meadows only *Sieglingia decumbens* and *L. multiflora* had relatively dense seed banks (a mean seed density over 250 seeds/m$^2$; Fig. 1.1). In contrast to graminoids, 25% of forbs detected in vegetation of fen meadows had any seed banks, and 18% were persistent. In dry-mesophilous meadows these scores were only 15% and 6%, respectively. Though some target species were only found in seed banks (e.g. some sedges like *Carex pilulifera* or *C. nigra*) these were significantly outnumbered by those ones which were exclusively found in vegetation. In fen-meadows 31 species (incl. protected species as *Achillea ptarmica*, *Gladiolus imbricatus*, *Gentiana pneumonanthe*) were exclusively found in above-ground vegetation, whereas in dry-mesophilous meadows this figure was 46 (incl. protected species such as *Carlina acaulis*, *Gentianella austriaca*). Overall, most of the detected legally protected target species (Király 2007) in both meadow types lacked persistent seed banks (9 out of 11 species). Only *Hypericum maculatum* (20-500 seeds/m$^2$) and *Carex hartmannii* (one seedling) had a detectable seed bank. Conversely, common rushes (*J. conglomeratus* and *J. effusus*), that were mostly missing from the vegetation, dominated the seed banks in all fen meadow plots (50-94% of total seed densities).

These rush species were also present in the seed bank in dry-mesophilous plots. Further rush species (*Juncus articulatus*, *J. bufonius*), several sedges (*Carex pilulifera, C. nigra, C. remota*), and a number of hygrophyte forbs (*Peplis portula, Scrophularia umbrosa, Typha angustifolia*) were exclusively detected in the seed banks.



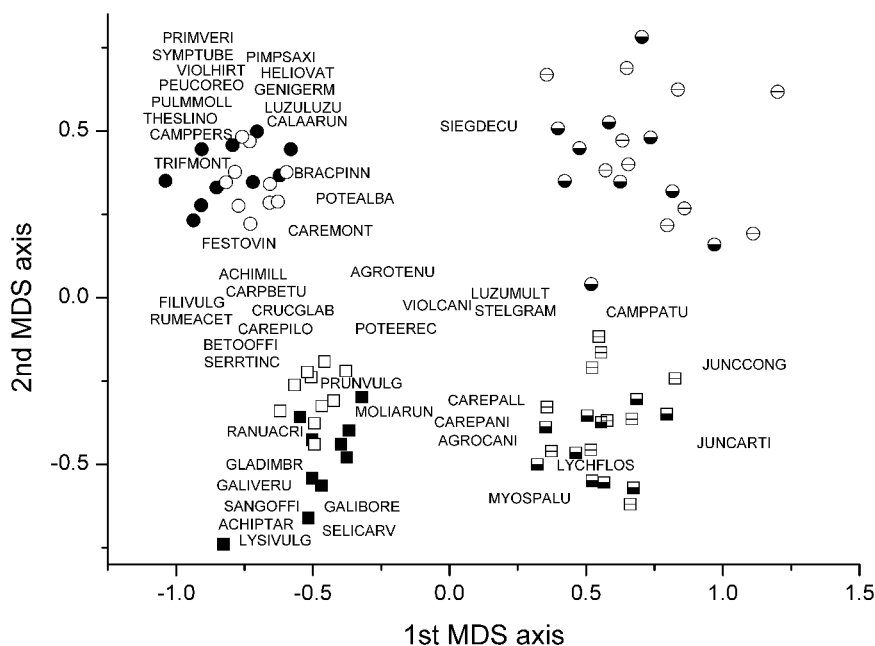**Fig. 1.1.** The similarity of vegetation and seed banks of fen meadow and dry-mesophilous meadow stands based on presence-absence of species (Sørensen similarity and MDS ordination, stress = 12.64). Notations: □ - fen meadow, vegetation, abandoned; ⊟ - fen meadow, seed banks, abandoned; ■ - fen meadow, vegetation, mown; ▬ - fen meadow, seed banks, mown; ○ - dry-mesophilous meadow, vegetation, abandoned; ⊖ - dry-mesophilous meadow, seed banks, abandoned; ● - dry-mesophilous meadow, vegetation, mown; ◓ - dry- mesophilous meadow, seed banks, mown.

## Discussion

### Vegetation and seed bank

The low to medium similarity between vegetation and seed banks reported here fit well in the range formerly detected in grasslands (Hopfensperger 2007; Bossuyt & Honnay 2008). Seed bank densities detected in the acidic dry-mesophilous meadows proved remarkably higher than in most analyzed dry-mesophilous calcareous grasslands (about 200-900 seeds/m$^2$; e.g. Kalamees & Zobel 1998; Willems & Bik 1998; Bossuyt et al. 2006), but somewhat lower than in some chalk grasslands in Germany (6,000-7,000 seeds/m$^2$; e.g. Poschlod & Jackel 1993). We detected seed densities in the soil of the fen meadows of an order of magnitude higher than in dry-mesophilous ones, which coincides with results of former studies conducted in similar wet meadow types (Bekker et al. 2000; Matus et al. 2003b; Jutila 2001). The enormously high seed density of the fen meadows was caused by the *Juncus* seeds. As in other wet meadows rushes comprised the largest part (50-94%) of the seed banks (most often *J. conglomeratus* and *J. effusus*; Bekker et al. 2000; Matus et al. 2003b; Jutila 2001). High loads of *Juncus* seed banks can threaten restoration but evidence is missing in what circumstances they really hamper the establishment of other species.

In contrast to the fen meadow stands the percentage of rushes in acidic dry-mesophilous meadows, measures as low as 2.2% of the seed bank (about a maximum of 130 seeds/m$^2$), similar to levels reported in previous studies on calcareous meadow types (Kalamees & Zobel 1998; Willems & Bik 1998). Total density of forbs was three to four times higher in fen meadows than in dry-mesophilous ones. This group contained the most target species and is often subject to extinction after abandonment (Stampfli & Zeiter 1999; Stammel et al. 2006). Furthermore, a much smaller proportion of these species had persistent seed banks in dry-mesophilous meadows, than in fen meadows. These results suggest that soil seed banks can only play a subordinate role in restoration of this meadow type.

### Management

Resumed traditional management is usually considered to promote species richness in vegetation of abandoned grasslands (Losvik 1999; Stampfli & Zeiter 1999; Williams et al. 2007). Our study also supports these findings. The picture, however, is less clear concerning reproductive success (flowering and seed banks). The flowering success of several species was apparently influenced by management.

It was difficult to judge whether or not resumed management could affect specific seed bank densities. The most likely reason is that the alteration of persistent seed bank is much slower than changes in vegetation (Ghorbani et al. 2007). Therefore, the seed bank structure and composition as a long-term 'successional memory' reflects the former stages of the vegetation development (Török et al. 2009).

*Conclusions*

Irrespective of the vegetation type only a small number of target species built up detectable seed banks. The same holds for the legally protected target species, which possessed at most sparse seed banks in both meadow types. Consequently, these species can become extinct locally when they disappear from the above-ground vegetation. Restoration of former species richness is therefore not possible from local seed banks. Our results demonstrated that in spite of the similar site conditions and vegetation, seed banks in the two meadow types were remarkably different. Consequently, restoration prospects also differ markedly. Regeneration of dominant grasses, sedges and several common forbs from local seed banks is promising in fen meadows, but it is still unknown whether or not high densities of pioneer *Juncus* seeds could hamper restoration aims. Poorly developed seed banks of dry-mesophilous meadows do not guarantee the regeneration of species-rich vegetation.

Spontaneous regeneration processes are increasingly integrated as restoration tools in ecological restoration (Prach & Hobbs 2008; Prach & Řehounková 2008). However, further case studies are needed to explore in which communities and circumstances could restoration actions be based on spontaneous recovering processes (e.g. spontaneous recovery from seed banks). Our results have demonstrated that even closely positioned stands of contrasting hay meadows require distinct restoration measures. In fen meadows one can rely on a spontaneous recovery of relatively species-rich stands resuming the former management. In contrast, propagule import is a further requirement for dry-mesophilous meadows (e.g. hay transfer from remaining species-rich stands; Donath et al. 2007; Wallin et al. 2009). Our results underline the importance of regular management for the species-rich hay meadows, as the most economic way of conservation. These stands also can serve as donor sites for improving degraded ones (Donath et al. 2007; Liu et al. 2009).

# Chapter 2

# Lucerne fields recover native grass diversity without intensive management actions

## Introduction

The aim of grassland restoration is to recover and/or improve grassland biodiversity and ecosystem functions (Firn 2007; Reid et al. 2009). Two contrasting approaches are used most often: technical reclamation or spontaneous succession (Prach & Hobbs 2008). Both methods are generally followed up by site management for weed suppression using techniques such as mowing and/or grazing (Warren et al. 2002; Lepš et al. 2007; Kiehl et al. 2010). Recovery can be accelerated and directed by *technical reclamation* methods. In most cases this means adding seeds of desirable species using hay transfer or seed sowing (Pywell et al. 2002; Hölzel & Otte 2003). An alternative approach is *spontaneous succession*, where seeds are not added and the system is left to recover naturally (Prach & Pyšek 2001). Technical reclamation is preferred worldwide despite several promising examples of spontaneous recovery of grasslands (e.g. Ruprecht 2006; Prach & Řehounková 2008). This is especially true when there is an urgent need to heal landscape scars, prevent erosion or suppress weeds (Török et al. 2010; Tropek et al. 2010).

Recently, there have been attempts to link theories of spontaneous succession with direct restoration efforts to mitigate costs and improve the success of restoration (Walker et al. 2007; del Moral et al. 2007). For example, patterns in vegetation dynamics could be used to judge whether or not invasive weed cover will develop rapidly after agriculture ceases or to judge whether active intervention is necessary to eliminate former crops. Spontaneous succession has several advantages over technical reclamation. (i) The natural value of spontaneously regenerated sites is often higher than that of reclaimed ones (Hodačová & Prach 2003). (ii) Spontaneously colonising species are expected to be better adapted to local conditions than species originating from commercial sources or non-local sites (van der Mijnsbrugge et al. 2010). (iii) Increased vegetation patchiness at spontaneously regenerated sites provides improved refugees for animals compared to technical reclamation sites (Tropek et al. 2010). Finally, (iv) spontaneous succession offers cost-effective restoration with a low rate of active intervention (Prach & Hobbs 2008).

Spontaneous succession also has some drawbacks compared to technical reclamation, concerning (i) the low level of predictability and control of initial vegetation composition, density and pattern, and (ii) the relatively slow development of vegetation towards to the target state, especially where proper donor sites for colonisation are missing (Ruprecht 2006; Prach & Hobbs 2008). However, the value of spontaneous succession in restoration programmes is becoming more widely appreciated, which underlines the importance of reporting relevant case (Prach & Pyšek 2001; Prach et al. 2001).

There is large scale abandonment in rural areas where productivity is low in Central- and Eastern Europe (Jongepierová et al. 2007; Török et al. 2010). After the collapse of state owned agricultural cooperatives, the socio-economical changes resulted in large scale abandonment of croplands (Prach et al. 2007; Pullin et al. 2009). Between 1990 and 2004, 600,000 hectares of croplands have been abandoned in Hungary (Hobbs & Cramer 2007). This has provided an opportunity to use these areas to restore grasslands and improve their continuity for nature conservation (Stevenson et al. 1995; Simmering et al. 2006; Lindborg et al. 2008).

Most studies reporting spontaneous succession have focused on abandoned fields formerly cultivated with annual crops or the previous history of the site (e.g. last crop) has been ignored (Csecserits & Rédei 2001; Ruprecht 2006). Generally in these studies, weedy short-lived species are found to dominate in the first years after abandonment (Blumenthal et al. 2005; Prach et al. 2007). Weed dominance is generally associated with high levels of soil nutrients, which can be difficult and costly to control (Blumenthal et al. 2003). The dominance of early colonising weedy species can also slow down the regeneration of target vegetation for many years (Collins et al. 2001; Prach & Pyšek 2001). Secondary succession after intensive cultivation of perennial crops has not previously been studied. One of the most important perennial crops worldwide is lucerne *Medicago sativa* L. Lucerne is often used as silage or hay for cattle forage (Horrocks & Valentine 1999; Li et al. 2007). In Hungary more than 130,000 ha of croplands were sown with lucerne although intensity of use has decreased in recent years (2004-2008; K.S.H. 2008).

*Aims of the study*

We studied the regeneration of loess grasslands in extensively managed (mown twice a year) lucerne fields using space for time substitutions. We addressed the following questions: (i) How effective is lucerne in weed control? (ii) How quickly does lucerne disappear? (iii) How fast does grassland recover in extensively managed lucerne fields? The overall aim of this study was to examine the value of

spontaneous succession in the restoration of grasslands in former lucerne fields as a cost-effective strategy for grassland conservation.


## Results

### *Vegetation and phytomass*

The vegetation of 1 and 3-year-old lucerne fields was characterized by the high cover of lucerne. Several weed species were present; their mean cover was less than 5% (e.g. *Conyza canadensis*, *Lamium amplexicaule*, *Polygonum aviculare, Stellaria media*). The mean cover of lucerne decreased from 75.2% to 2.2% with increasing field age. In the vegetation of 5-year-old fields the cover of lucerne was lower than 50% in all studied plots; moreover in one of the 10 year old fields no lucerne cover was detected. Conversely, the mean cover of perennial graminoids increased from 0.5% to 50.2% parallel with increasing field age (GLMM, $P<0.001$, d.f.=134, $t$=14.30; Table 2.1). The mean total cover of differently aged lucerne fields fluctuated between 77.6% and 86.1% (Table 2.1). Altogether 104 vascular plant species were recorded in the vegetation of the studied lucerne fields. The mean total species richness (from 8.5 to 13.9-14.7), the mean species richness of perennials (from 2.4 to 5.8-6.0), and the mean Shannon diversity scores (from 0.5 to 1.5-1.6) were increased with field age (GLMM, $P<0.001$, d.f.=134, $t$=11.04 and 11.17, respectively; Table 2.1).

No significant differences were found between the total phytomass of differently aged lucerne fields (means ranged between 286-689 g/m$^2$). As for cover, the phytomass of lucerne decreased with increasing field age (GLMM, $P<0.001$, d.f.=350, $t$=17.17). The phytomass of graminoids was highest in the 5 and 10-year-old fields (Fig. 2.1). A negative correlation was detected between the phytomass of lucerne and that of graminoids. Litter and forb phytomass were also negatively correlated, but no clear temporal trend was detected. A decreasing lucerne phytomass and an increasing grass phytomass were detected with increasing field age (Fig. 2.2.)

**Table 2.1.** Cover, species richness and Shannon diversity scores of functional species groups. Different superscripted letters indicate significant differences tested with GLMM and Tukey test ($P<0.05$).

| | Age of lucerne fields | | | |
|---|---|---|---|---|
| | 1-yr-old | 3-yr-old | 5-yr-old | 10-yr-old |
| **Cover** (%, mean±SE) | | | | |
| Total | 85.4±0.4 | 85.8±4.7 | 86.1±12.9 | 77.6±12.6 |
| *Medicago sativa* | 75.2±1.1[a] | 72.8±11.0[a] | 24.1±4.9[b] | 2.3±2.3[c] |
| Perennial forbs (excl. *M. sativa*) | 0.7±0.2[a] | 6.5±4.5[b] | 10.7±2.7[b] | 16.3±2.2[c] |
| Perennial graminoids | 0.5±0.2[a] | 0.9±0.1[a] | 29.8±14.1[b] | 50.2±15.0[c] |
| Short-lived forbs | 8.9±1.6 | 5.4±2.2 | 10.6±7.6 | 6.2±0.5 |
| Short-lived graminoids | 0.1±0.1[a] | 0.2±0.1[a] | 11.0±3.9[b] | 2.6±1.5[a] |
| **Species richness** (mean±SE) | | | | |
| Perennial species | 2.4±0.2[a] | 3.3±0.4[a] | 6.0±1.1[b] | 5.8±0.4[b] |
| Short-lived species | 6.1±0.7[a] | 5.2±1.6[a] | 8.7±2.1[b] | 8.1±1.0[b] |
| Shannon diversity | 0.5±0.1[a] | 0.6±0.3[a] | 1.6±0.2[b] | 1.5±0.2[b] |
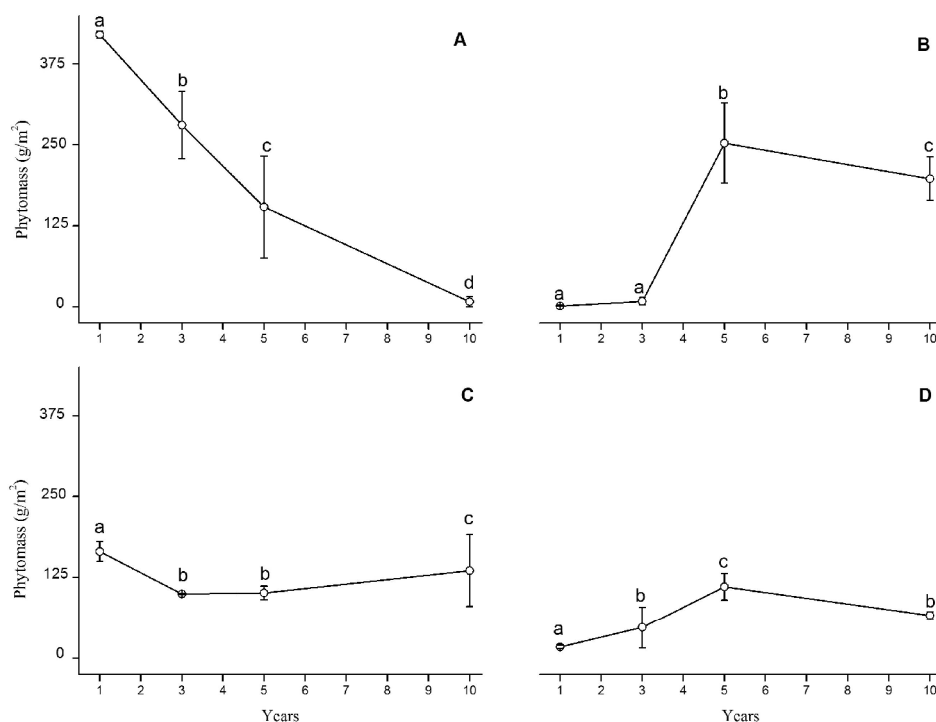


**Fig. 2.1.** Phytomass scores of *Medicago sativa* and three functional groups in differently aged lucerne fields. Notations: A = *Medicago sativa*, B = graminoids, C = litter, D = other forbs. Different letters indicate significant differences within a phytomass group between years (GLMM and Tukey test, $P<0.05$; tests were executed on 20×20cm samples).

*Lucerne fields and reference grasslands*

Characteristic grass species for reference grasslands (e.g. *Festuca rupicola* and *Bromus inermis*) were found at low levels of cover in 5 and 10-year-old lucerne fields. Conversely, some common grasses were dominant (e.g. *Festuca pseudovina, Poa angustifolia, Elymus repens, Alopecurus pratensis*). Decreasing mean dissimilarity of species composition was detected with increasing field age (from a mean of 0.96 in 1-year-old fields to a mean of 0.76 in 10-year-old fields). Characteristic forb species of target loess grasslands were only present in 5 and 10-year-old lucerne fields (e.g. *Vicia hirsuta, V. angustifolia, Galium verum, Medicago minima, Trifolium angulatum, T. retusum, Lathyrus tuberosus*).
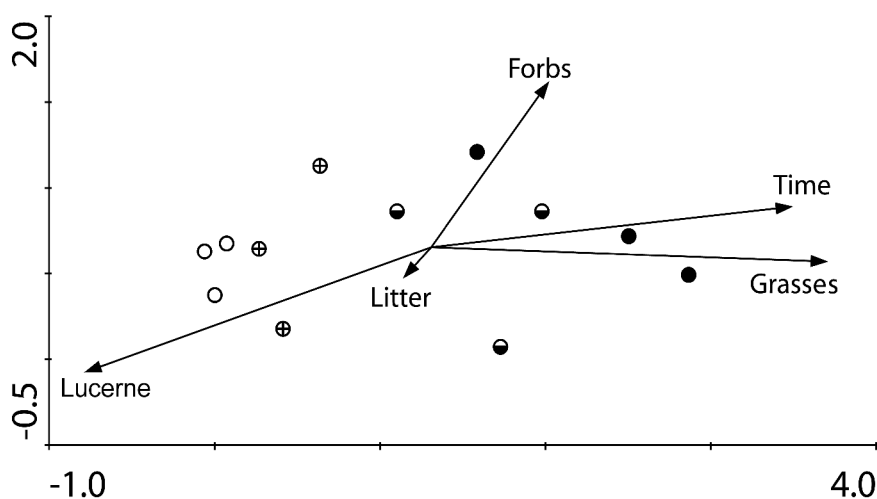


**Fig. 2.2.** The relationship between the various phytomass fractions and time using DCA. The points (main data) were based on mean species percentage cover. All data were pooled at the field's level. Notations for the lucerne fields: 1-year-old - ○; 3-year-old - ⊕; 5-year-old - ⊖; 10-year-old - ●. Notations for the background variables (arrows): Lucerne = phytomass of lucerne; Forbs = forb phytomass; Grasses = graminoid phytomass, Time = field age; Litter = litter phytomass. Eigenvalues are 0.52 and 0.08 for axis 1 and 2, respectively.

Several other characteristic perennial forbs were not detected even in the vegetation of 10-year-old lucerne fields (e.g. *Ajuga genevensis, Salvia nemorosa, S. austriaca, Pimpinella saxifraga, Thymus degenianus, Euphorbia cyparissias, Veronica prostrata*). Several disturbance tolerant and weedy perennial forbs were

more frequent in the lucerne fields than in reference grasslands (e.g. *Cirsium arvense*, *Convolvulus arvensis*, *Taraxacum officinale*). Species composition in the lucerne fields showed a clear shift along the first axis in the NMDS ordination (Fig. 2.3). Time is represented by the first axis, and the age groups are separated along it. The vegetation of the 1 and 3-year-old fields showed low variability, while the variability of plots of the older fields was much higher (Fig. 2.3). The vegetation of the 10-year-old fields showed the most similarity with the vegetation of reference grasslands.
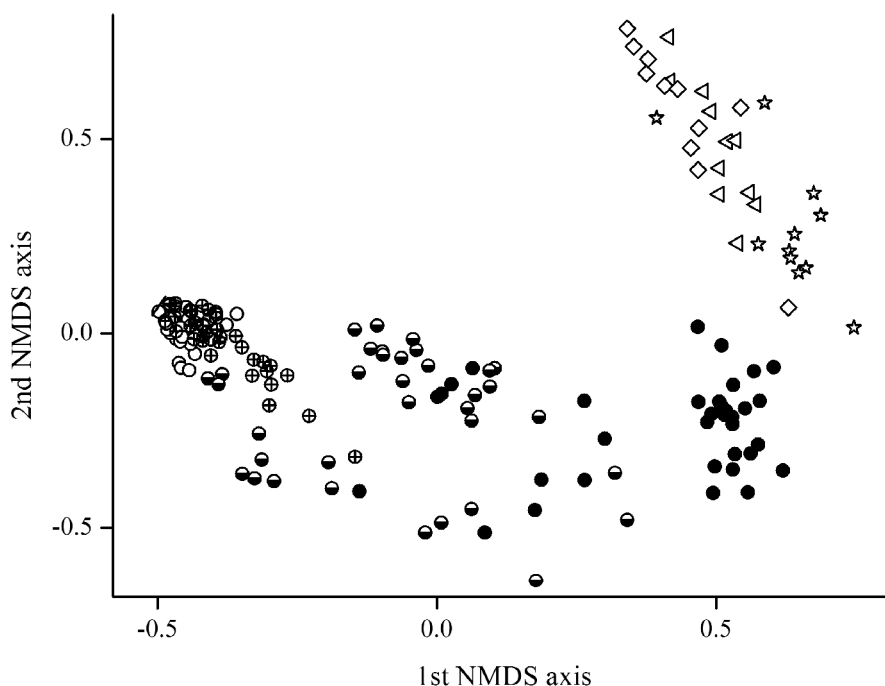


**Fig. 2.3.** Vegetation composition of differently aged lucerne fields and reference grasslands. Ordination plot was based on percentage cover data of the sample plots using NMDS ordination and Bray-Curtis similarity (Stress = 15.91). Lucerne fields: 1-year-old - ○; 3-year-old - ⊕; 5-year-old - ◓; 10-year-old - ●; Species poor Cynodonti-Poëtum loess grassland - ◇; Loess balk with high cover of *Bromus inermis* - ☆; Species rich Salvio-Festucetum loess grassland - ◁.

**Discussion**

*Weed control*

Previous studies have reported high weed cover after abandonment of intensively managed croplands, e.g. weed cover of 5-40% for sandy fields abandoned for 1 to 10 years (Central-Hungary; Csecserits & Rédei 2001; Csecserits et al. 2007), and 10-60% for 1 to 12-year-old abandoned loess fields (Ruprecht 2005, 2006). Low weed cover was found after abandonment only where crop production lasted just a few years, and no mineral fertilizers had been applied (e.g. Jongepierová et al. 2004). It has been suggested that the rapid development of weed cover can be avoided by sowing mixtures of seeds of characteristic late successional species (Prach & Pyšek 2001; Pywell et al. 2002; Warren et al. 2002) or cover crop grasses (Hansson & Fogelfors 1998).

In our study weedy species did not dominate in the early years. The total cover of weeds was low at less than 5% cover, regardless of the age of the fields. Our results support the findings of Li et al. (2007), where legume species such as lucerne were found to aid in suppressing weeds. It is well known that seeds of weed species are present in the soils of croplands in high density (Hutchings & Booth 1996; Manchester et al. 1999). Török et al. (2010) detected a high cover of short-lived weeds after ploughing and sowing of perennial graminoids in former lucerne fields (1 to 3 years old), which suggests a high amount of weed seeds in the soil of lucerne fields. The low cover of weeds detected in the present study is most likely to be explained by the presence of lucerne, than by the absence of weed seeds in the soil. The high cover and phytomass of lucerne in the first years caused weed suppression by increased shading of the soil surface (Güsewell & Edwards 1999), and/or the competitive exclusion of short-lived weeds (Bischoff et al. 2005). An allelopathic effect of lucerne may be responsible for low weed cover: Ells & McSay (1991) showed that lucerne leaf extract (containing phenolic allelochemicals) was detrimental to germination and differentiation of susceptible plants.

*Cover and phytomass of lucerne*

In our study the cover of lucerne was over 70% in 1 and 3-year-old lucerne fields. A sharp decline was detected after the third year. This is in accordance with the common agricultural practice in this region, where the lucerne is re-sown after 3-4 years of cultivation. In a sowing experiment conducted by Li et al. (2007) in loess plateaux in China, the mean cover of lucerne decreased after the first year of sowing (about 50% of cover in the first, and 29% in the third year after sowing,

respectively). The more rapid decrease in lucerne cover can be explained by the lower sowing density than in our study (22.5 kg/ha, in our region 30 kg/ha is typical). Our results suggest that lucerne could disappear within a decade from grasslands under extensive management by mowing. The disappearance of lucerne could also be facilitated by low intensity grazing, which would select for leguminous species (Stroh et al. 2002).

In previous studies a significant increase in total vegetation cover (Li et al. 2008; Ruprecht 2005) or an increase of cover and/or phytomass of perennials (Štolcová 2002; Feng et al. 2007a,b; Török et al. 2008a) has been found during secondary succession. In our study, no such trend was detected. The total cover and also the total phytomass scores remained stable during secondary succession. This was caused by the gradual replacement of lucerne by perennial grasses. Török et al. (2010) found litter accumulation of one order of magnitude higher between the first and second years after restoration of grasslands with low diversity mixtures in former lucerne fields (first year litter: 28-37g/m$^2$; second year litter: 280-289 g/m$^2$). The litter scores in the second and the third year of this study were about 2-3 times higher than that detected in the present study. Accumulated plant litter was identified as negatively affecting vascular plant species richness in several studies (Huhta et al. 2001; Enyedi et al. 2007). Therefore, high amounts of litter with high perennial cover is especially effective in weed suppression (Török et al. 2009). Litter accumulation can also be negative as litter can reduce the micro-topographical heterogeneity (Tropek et al. 2010), and decrease the availability of colonisation sites (Jensen & Gutekunst 2003), which can stabilise the community in an undesirable state (Hobbs et al. 2006). High amounts of litter could also hamper the immigration and establishment of several target species by limiting microsite availability (Foster & Gross 1998; Bissels et al. 2006). In this study, there was no litter accumulation detected and, as a result, germination and colonisation was not hampered and species richness increased with field age. Other studies reporting spontaneous grassland succession have found similar links with litter accumulation and reduction in germination and colonisation (Jongepierová et al. 2004; Ruprecht 2006; Feng et al. 2007a).

*Recovery of grasslands*

We found that the recovery of species poor loess grasslands dominated by perennial native species in former lucerne fields was possible within 10 years. Other old-field studies found 6-23 years after abandonment was sufficient time for the spontaneous succession of loess grasslands (Molnár & Botta-Dukát 1998; Ruprecht 2005; Csecserits et al. 2007; Feng et al. 2007a,b). The dissimilarity in species

composition between lucerne fields and reference grasslands has continuously decreased with increasing field age. Dissimilarity scores were, however, high even between 5 and 10-year-old fields and reference grasslands. Several perennial forbs found at high frequency in loess grasslands were not detected in lucerne fields; and several short-lived weeds detected with low cover but high frequency in lucerne fields were missing from reference grasslands (see Appendix 2.1). Previous studies have reported that the spontaneous immigration of desirable target species is a diaspore limited process (Donath et al. 2007; Kiehl et al. 2010). There are two reasons for diaspore limitation: 1) limited spatial dispersal (e.g. missing dispersal agents and heavy seeds) reduces the movement of seeds into target sites (Simmering et al. 2006); 2) long-term agricultural use often depletes the local seed bank, and also increases the amount of weed seeds in the soil (Coulson et al. 2001). Therefore, spontaneous recovery will be most effective where target grassland sites are located nearby (Öster et al. 2009). A further explanation for the persistent differences in species composition between the old fields and reference grasslands is that the perennial forbs may require more time to establish in extensively managed fields (e.g. Prach et al. 2007).

*Practical implications for policy*

Our results suggest that the recovery of initial loess grasslands may not require technical reclamation methods (i.e. sowing competitor grasses and/or forbs) in lucerne fields where nearby grasslands are present as a seed source. We found that after a decade of regular mowing, lucerne fields were transformed into loess grasslands dominated by native perennial grasses. However, most of the characteristic loess grasslands forbs are missing. Similar results were found under the more common technical reclamation method of sowing low diversity seed mixtures (Hansson & Fogelfors 1998; Lepš et al. 2007; Török et al. 2010). The full recovery of loess grasslands requires more time and/or should be facilitated by technical introduction of some of the target species (Kirmer et al. 2008; Kiehl et al. 2010). The transfer of hay and/or low intensity grazing combined with continued mowing can be another option to facilitate the establishment of desirable species.
Our results suggest that sowing lucerne in abandoned fields and following this with extensive management can combine the advantages of both spontaneous succession and technical reclamation in grassland restoration. It offers a cost effective solution from the economic (agricultural) and conservation management point of view. The method has several advantages over technical reclamation. In particular, there is no weed dominated stage and no intensive litter accumulation. Lucerne gradually decreases in abundance once re-sowing and/or fertilizing stops so there will be a

lower microsite limitation rate compared to technical reclamation sites where competitor grasses are sown. Finally, spontaneous succession is cheaper than technical reclamation, and provides a high value hay harvest in the first few years in lucerne fields.

# Chapter 3

# Grassland restoration by sowing low-diversity seed mixtures in former lucerne fields

## Introduction

Agricultural intensification and overproduction often leads to the abandonment of croplands in Europe and elsewhere (Ramankutty & 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 & 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 & 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 & Walker 2007).

The most trivial method to restore grasslands is based on spontaneous processes (old-field succession, Prach & Pyšek 2001). The regeneration of the former grassland vegetation, however, is often slow and highly unpredictable (Hutchings & Booth 1996). Regeneration is often hindered by the lack of propagules of species of conservation value due to seed bank depletion (Hutchings & 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 & Redente 1992; Prach & Pyšek 2001). Therefore,

more active conservation often attempts to control and accelerate successional changes (Luken 1991; Pakeman et al. 2002) by sowing propagules 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.

*Aims of the study*

We studied the early successional changes after grassland restoration on croplands previously used as lucerne fields. Lucerne 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 lucerne 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. The loess seed mixture contained *Festuca rupicola*, *Poa angustifolia* and *Bromus inermis*, whereas the alkali seed mixture contained *Festuca pseudovina* and *Poa angustifolia*. 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) Can weeds be suppressed by sowing competitive native grasses, followed up by management by

mowing? (ii) How fast does the cover of sown grasses develop after sowing low diversity seed mixtures? (iii) Can succession towards the target 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.

## Results

### *The regeneration process*

In Year 1 of the study (2006), short-lived weedy forb species dominated the restored fields (*Capsella bursa-pastoris*, *Matricaria inodora*, *Polygonum 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 (Appendix 3.1). 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 forbs have decreased significantly during the three years of secondary vegetation development, whereas that of perennial grasses increased (Appendix 3.1)

**Table 3.1.** Phytomass scores 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 plot 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 |
| Forb | *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] |
| Non-sown 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] |

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, *Poa angustifolia* had a cover > 5% in six sites already in Year 1. From Year 1 to 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 (Appendix 3.1, Fig. 3.1). Several unsown perennial grass species (*Elymus repens*, *E. hispidus*, *Festuca 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: *Silene viscosa*, *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*).
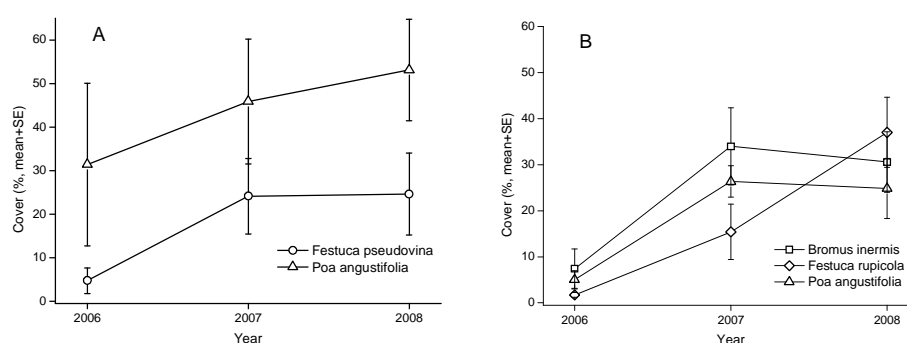


**Fig. 3.1. A-B.** Changes in percentage cover of sown species between Year 1 (2006) and Year 3 (2008) in restored fields using alkali seed mixture (A) and loess seed mixture (B). Data are from six sites restored using loess mixture (pooled samples at plot level, n = 6) and from four sites restored using alkali mixture (pooled samples at plot level, n = 4; mean±SE).

*Species richness and phytomass*

A total of 95 species were recorded in the plots of the restored fields in the three years. Of all detected species, 23 were graminoids, and 72 were forbs. Most forbs were short-lived; only 15 perennial species were detected, each of them with low cover. We detected 67 species (15 graminoid, 52 forb) in alkali plots, and 79 species (20 graminoid, 59 forb) in loess plots. Total species richness decreased significantly from Year 1 to 2 in both types of restoration (Appendix 3.1). From

Year 2 to 3, a low but significant increase in species richness occurred in the loess plots, but not in the alkali plots (Appendix 3.1). Shannon-diversity was highest in Year 1 and decreased from Year 1 to 2 in both types of restoration. Diversity increased back again from Year 2 to 3 in loess plots, but not in alkali plots.
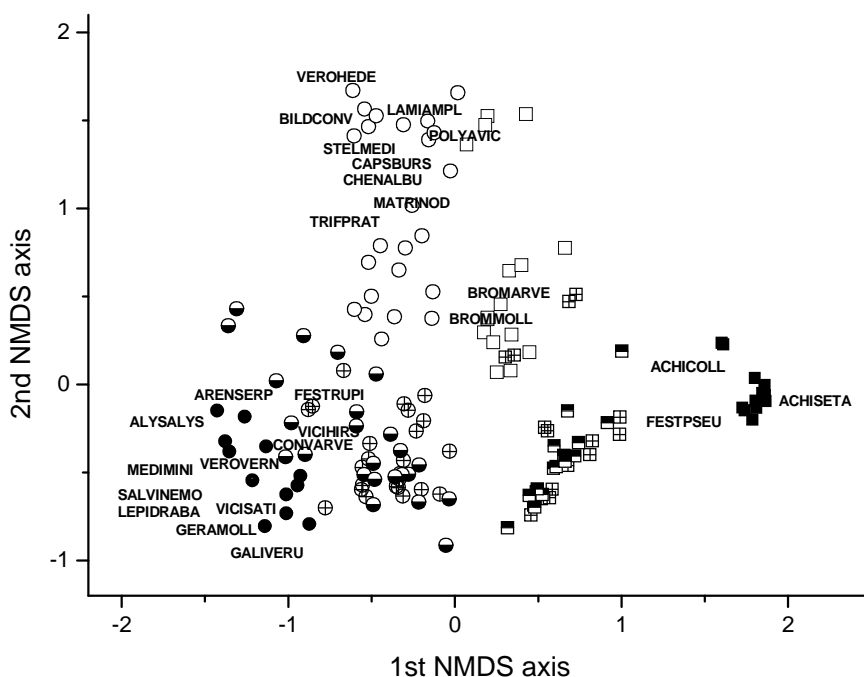


**Fig. 3.2.** Similarity between reference grasslands and the restored fields based on the percentage cover of species (Bray-Curtis similarity and NMDS ordination; stress = 21.34). Alkali seed mixture: 2006: □, 2007: ⊞, 2008: ▭, reference alkali grassland: ■. Loess seed mixture: 2006: ○, 2007: ⊕, 2008: ◓, reference loess grassland: ●. Species with IndVal scores higher than 50 were plotted. Species are abbreviated using four letters of the genus name and four letters of the species name.

The changes in phytomass were similar in both types of restored fields. Forb 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 ten-fold increase in litter was observed from Year 1 to 2 and 3. The phytomass of the grasses sown gradually increased during succession (Table 3.1).

*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. 3.2). 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 Year 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. 3.2). The increasing homogenisation of species composition of various alkali plots corresponded well with the high internal homogeneity of the target alkali grasslands (Fig. 3.2).

**Discussion**

*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; Jongepierová et al. 2007). The short-lived weeds, however, were rapidly replaced by perennial species, and already in Year 2 the perennials 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, 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 Year 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 & Tilman 2000; Anderson 2007). This process is also promoted by high nutrient levels in the soil (Marrs 1993; Huston 1978). 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 forb species were detected in the first year in both types of restored fields ($28\text{-}38\text{-g/m}^2$). 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 ($220\text{-}268\text{-g/m}^2$ in the restored fields and $62\text{-}160\text{-g/m}^2$ in managed alkali and loess grasslands, Deák et al. 2011). 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 Year 1 to Year 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 & 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 & Gabrielson 1985; Bartha 2001).

Parallel to the disappearance of short-lived species, several perennial unsown graminoids became established in the restored fields (*Festuca pratensis*, *Elymus hispidus*, *E. repens*). These species frequently occur in lucerne 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 & Gabrielson 1985).

*Development of perennial grass cover*

The theory of "slowing down succession" suggests that the vegetation development slows down after the formation of perennial dominance (Inouye et al. 1987; Lepš 1987; Foster & 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 Year 2 and Year 3 than in Year 1 to Year 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 *Festuca rupicola*, *Poa angustifolia* and *Koeleria cristata*) was reported only after 10 years (Molnár & Botta-Dukát 1998). Ruprecht (2005) reported cover values of *Festuca rupicola* similar to that found here in 10- to 14-year-old spontaneously regenerating old-fields. After heavy goose browsing, the perennial graminoid dominance was established spontaneously in bare, nutrient-rich sandy soil only after 4-7 years of secondary succession (*Festuca pseudovina*, *Poa angustifolia* and *Cynodon dactylon*, Matus et al. 2005; Török et al. 2008a). In another sandy old-field study in the Great Plains area in central Hungary, the mean cover of perennials exceeded 50% only in 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 to 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 & 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. 3.2). 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.

*Recruitment of desirable species – implications for restoration*

We detected a slow spontaneous immigration of forb species characteristic to reference grasslands. This is in accordance with the findings of other studies of grassland restoration in former croplands (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 dominance following the abandonment of agricultural cultivation. Vegetation dominated by perennial grasses, which prevents the long-term establishment of weedy species, developed rather quickly, in three years. Even the sowing of low-diversity seed mixtures can quickly lead to seminatural grasslands when the starting conditions (less disturbed lucerne fields with adjacent propagulum sources) and management options are carefully matched. Therefore, this method proved to be effective in the restoration of target 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 specialist in the restored fields and eliminate the negative effects of limited spontaneous dispersal (Hölzel & Otte 2003; Donath et al. 2006; Leng et al. 2009).

# Chapter 4

# Litter and graminoid phytomass accumulation suppresses weedy forbs in grassland restoration

## Introduction

In many parts of the world, the decreasing rate of crop production favours grassland restoration actions in former croplands (Csecserits & Rédei 2001; Cramer et al. 2008). The major goals in such projects are (i) to suppress early colonising assemblages by late successional ones, (ii) restore native grassland diversity and (iii) restore ecosystem functions (Reid et al. 2009; Török et al. 2010). To meet these goals, it is often necessary to control the dry matter production in the recovered grasslands by different management techniques (Házi et al. 2011). Thus, the study of dry matter production in seminatural and restored grasslands has become an important research topic in restoration ecology (Bischoff et al. 2005, Guo 2007).

The relation of total aboveground phytomass and species richness can be often described by a hump-shaped curve where a negative correlation can be observed if high phytomass scores are measured (Grime 1979; Oomes 1992; Guo 2007). Old-fields and restored grasslands can be characterised typically by higher phytomass production than natural grasslands (Carson & Barrett 1988) because of a high residual nutrient content that regularly occurs following the termination of agricultural activity (Huston 1999; Csecserits et al. 2011). In turn, high phytomass production often results in a high rate of litter accumulation (Odum 1960).

Litter and graminoid phytomass plays a crucial role in grassland dynamics (Martin & Wilsey 2006). Increased graminoid phytomass and accumulated litter usually inhibits germination (Foster & Gross 1998) by reducing the irradiance of the soil surface (Foster & Gross 1997), forming a physical barrier (Wedin & Tilman 1993), or altering the competitive environment (Kotorová & Lepš 1999; Rotundo & Aguiar 2005). A dense litter layer decreases the average soil temperature and reduces the variability of temperature by mitigating extreme fluctuations (Eckstein & Donath 2005), which decreases the germination rate of most forb species (Jutila & Grace 2002; Donath et al. 2006). Furthermore, increased graminoid production and litter reduce the amount of available water for forbs (Haugland & Froud-Williams 1999), although it may also help in preserving soil moisture under arid conditions (Fowler 1988). Nutrients (Facelli & Pickett 1991) and allelopathic compounds can be dissolved from the litter, which negatively affects overall diversity (Bonanomi et

al. 2005; Ruprecht et al. 2008). From a conservation standpoint, it is a positive effect that graminoid phytomass and litter may suppress the early colonising weedy forbs that are abundant after abandonment.

Here we study the effects of litter and phytomass of sown grasses on species richness and phytomass of early colonising forbs in former lucerne fields sown with low-diversity seed mixtures in NE Hungary. Sowing low-diversity seed mixtures of native, competitive grass species followed by regular mowing is an effective method in grassland restoration because weedy forbs are usually rapidly replaced (Lepš et al. 2007). However, most studies analyse only changes in cover and species richness and changes in phytomass are typically neglected.

## *Aims of the study*

Here we measured both species richness and phytomass of litter, forbs, and sown grasses in the first three years after sowing and asked the following questions: (i) What is the effect of the accumulating phytomass of graminoids and litter on the phytomass of early colonisers? (ii) Is the amount of graminoid phytomass and litter higher, and the heterogeneity of these scores lower in sown fields than in natural grasslands? (iii) Is the amount of forbs lower in restored fields than in target grasslands?

## **Results**

### *Temporal change of phytomass in sown fields*

Total phytomass decreased significantly in restored fields from Year 1 to Year 2 regardless to the seed mixture sown (from a mean range of 1459-1480 $g/m^2$ to 696-789 $g/m^2$, RM ANOVA, alkali seed mixture: $N=4$, $F=6.27$, $p=0.034$, and for the loess seed mixture: $N=6$, $F=33.44$, $p<0.001$, respectively). A significant increase in total phytomass was detected between Year 2 and Year 3, but these figures were lower than the scores detected in the first year in both mixtures sown fields. The phytomass of the sown graminoids increased continuously, and the detected scores were typically more than two times higher in Year 3 than in Year 1 (RM ANOVA, alkali seed mixture $N=4$, $F=10.00$, $p=0.012$, and loess seed mixture: $N=6$, $F=7.68$, $p=0.01$, Fig 4.1). Total graminoid phytomass was highest in Year 3, coinciding with the increase of sown grasses in both types of mixtures (RM ANOVA, alkali: $N=4$, $F=27.83$, $p<0.001$; loess: $N=6$, $F=12.09$, $p=0.002$, Fig 4.1).
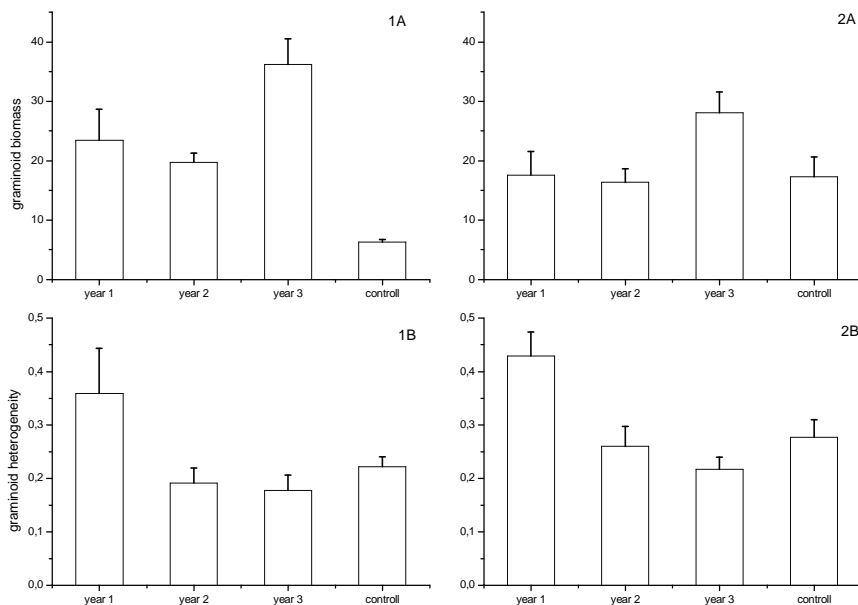
**Fig. 4.1.** Phytomass (A) and phytomass heterogeneity (B) scores of graminoids in alkali seed mixtures (1), and loess seed mixtures (2) sown fields (mean±SE). Scores for native grasslands are shown in the last column in every subfigure (in 1A and 1B subfigure scores for alkali, in 2A and 2B scores for loess native grasslands are shown).

A significant litter accumulation was observed from Year 1 to Year 2 in every restored field. Litter scores increased by one order of magnitude (RM ANOVA, alkali seed mixture: $N=4$, $F=8.24$, $p=0.019$, loess seed mixture: $N=6$, $F=5.06$, $p=0.03$; Fig. 4.2). No significant changes were found in litter scores between Year 2 and Year 3, regardless of the seed mixture sown. Forb phytomass in Year 1 was dominated by short-lived weeds in every field; regardless of the seed mixtures sown (mean proportions were 99 % for the alkali and 95 % for the loess seed mixture). Forb phytomass (incl. weeds) decreased significantly in every restored field from Year 1 to the Year 2, typically by two orders of magnitude, regardless of seed mixture (RM ANOVA, alkali seed mixture: $N=4$, $F=9.59$, $p=0.014$; loess seed mixture $N=6$, $F=52.93$, $p<0.001$). Phytomass scores of forbs remained low (less than 18 g/m$^2$ in every sown field) from Year 2 onwards. Coinciding with the decrease of forb phytomass, the species numbers of forbs also decreased both in alkali and loess restorations from Year 1 to Year 2, and remained stable and low from Year 2 onwards (RM ANOVA, alkali seed mixture: $N=4$,

$F$=151.68, $p$<0.001; loess seed mixture: $N$=6, $F$=38.50, $p$<0.001). In most fields, graminoid phytomass and litter were negatively correlated with forb species richness and phytomass. Forb phytomass and species richness showed a medium strong negative correlation with graminoid phytomass and a strong negative correlation with litter (Table 4.1).

**Table 4.1.** Correlation coefficients ($r$) between species richness and phytomass of forb group and the amount of litter and sown grass phytomass by Spearman non-parametric rank correlation. Notations: ***- $p$ <0.001, **- $p$ <0.01, *- $p$ <0.05, n.s. - non-significant, $N$ = 12; 4 plots per field and three years. Field abbreviations: AM1-4: Alkali seed mixture restored fields, LM1-6: Loess seed mixtures restored fields.

|  | Field code | $p$ | Sown graminoid phytomass | $p$ | Litter |
|---|---|---|---|---|---|
| **Forb phytomass** | AM1 | *** | -0.62 | *** | -0.75 |
|  | AM2 | ** | -0.51 | ** | -0.65 |
|  | AM3 | * | -0.43 | *** | -0.64 |
|  | AM4 | n.s. | -0.17 | *** | -0.63 |
|  | LM1 | n.s. | 0.17 | * | -0.45 |
|  | LM2 | *** | -0.66 | *** | -0.84 |
|  | LM3 | n.s. | -0.18 | *** | -0.64 |
|  | LM4 | n.s. | -0.32 | ** | -0.56 |
|  | LM5 | * | -0.37 | *** | -0.66 |
|  | LM6 | * | -0.41 | *** | -0.59 |
| **Forb species richness** | AM1 | *** | -0.71 | *** | -0.80 |
|  | AM2 | ** | -0.47 | *** | -0.67 |
|  | AM3 | * | -0.37 | *** | -0.71 |
|  | AM4 | n.s. | -0.17 | *** | -0.67 |
|  | LM1 | n.s. | 0.31 | n.s. | -0.37 |
|  | LM2 | *** | -0.67 | *** | -0.85 |
|  | LM3 | n.s. | -0.12 | *** | -0.65 |
|  | LM4 | n.s. | -0.35 | ** | -0.55 |
|  | LM5 | * | -0.38 | ** | -0.57 |
|  | LM6 | ** | -0.53 | ** | -0.57 |

*Sown fields and target grasslands*

In Year 3, we observed significantly higher graminoid phytomass in alkali restorations compared to target alkali grasslands (one-way ANOVA, $N$=10, $F$=27.40, $p$<0.001). The mean scores of graminoid phytomass detected in the alkali restorations ranged from 616 to 1112 g/m$^2$, whereas these scores were much lower

in target grasslands (range 140 - 178 g/m$^2$). In loess restorations, graminoid phytomass scores (range 468 - 987 g/m$^2$) were not significantly higher than that of the target loess grasslands (range 262 - 520 g/m$^2$), although high scores were more common in loess restorations.
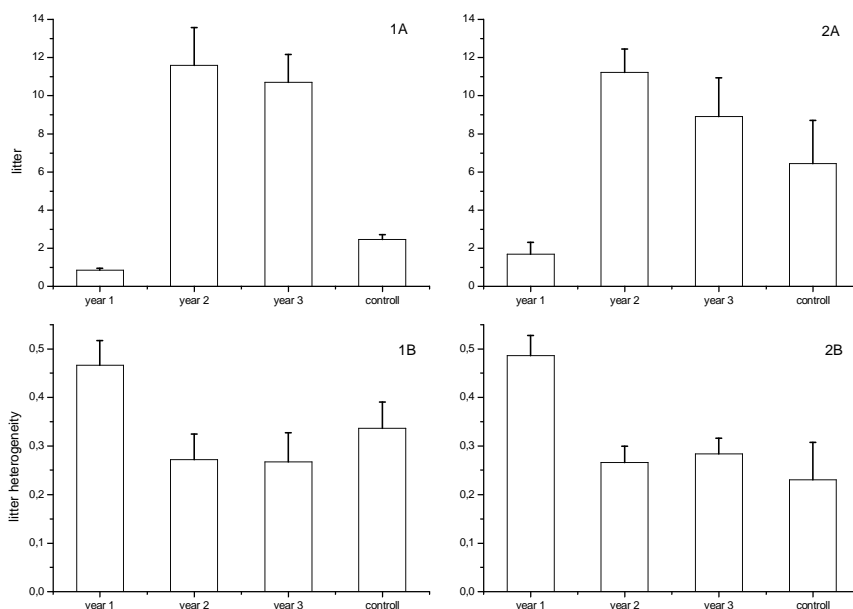


**Fig. 4.2.** Litter (A) and litter heterogeneity (B) scores for graminoid phytomass in alkali seed mixtures (1), and loess seed mixtures (2) sown fields (mean±SE). Scores for native grasslands are shown in the last column in every subfigure (in 1A and 1B subfigure scores for alkali, in 2A and 2B scores for loess native grasslands are shown).

In Year 3, significantly higher litter scores were found in alkali restorations than in target alkali grasslands (one-way ANOVA, $N=10$, $F=14.94$, $p<0.001$). The detected mean scores of litter were three to five times higher in alkali restorations than in target alkali grasslands (ranges 175 - 353 in restorations and 51 - 72 g/m$^2$ in target grasslands). Similarly to the graminoid phytomass scores, no significant differences were found in the litter scores between loess restorations and target loess grasslands, although scores were slightly higher in the sown fields (range 130 - 466 g/m$^2$ in restorations and 95 - 273g/m$^2$ in target grasslands).

The heterogeneity of litter and graminoid phytomass was highest in Year 1, and much lower scores were typical in both restorations in later years (Fig. 4.1 and

4.2). No significant differences were found between the heterogeneity of litter and graminoid phytomass in Year 3 in restorations and in target grasslands.

## Discussion

### *Changes in phytomass and litter*

This study provided three key results. First, we found significantly lower forb phytomass in the second and third year, than in the first year after sowing. Second, litter and phytomass of graminoids increased significantly during the study, and correlated negatively with the phytomass and species richness of forbs. Finally, mean scores of litter and graminoid phytomass were 2-3 times higher in sown fields than in target grasslands.

In our study, the highest total phytomass scores were detected in the first year, conversely to Lepš et al. (2007), where an increase of phytomass was detected after sowing from the first year to the second. In the study of Lepš et al. (2007), the mean total phytomass scores were at 300 $g/m^2$ in the first year; these scores increased in the second year to 430-720 $g/m^2$ depending on the used mixture and/or management. In our study, the first year's scores were at least four times higher than in the mentioned study (up to 1480 $g/m^2$). This difference was caused by the rapid development of weedy forb-dominance in the first year detected in our study. In the second year similar scores were also typical in our study, which suggested that the rate of suppression was poorly correlated with the first year phytomass.

Similarly to our study, a rapid increase in cover and richness of sown late-successional species was detected in former studies of grassland restoration using seed sowing (Pywell et al. 2002; Foster et al. 2007; Lepš et al. 2007). Our results confirmed that this increase of sown species holds also for the increase of their phytomass. We detected a rapid accumulation of graminoid phytomass and litter in the first three years of grassland restoration. Such a rapid increase of late-successional species was not detected in studies concerning spontaneous succession in old fields (Prach & Pyšek 2001; Bartha et al. 2003; Ruprecht 2006; Csecserits et al. 2007). The detected rapid phytomass increase also supports the theory that the speed and success of grassland recovery likely limited by diaspore availability of grassland species. Seed sowing is suggested to overcome the diaspore limitation (Pywell et al. 2002; Donath et al. 2003) and is recommended for directing vegetation changes if necessary (Lepš et al. 2007).

Despite of the regular yearly mowing, we detected a litter accumulation between the first and second year. The litter scores increased from 21-42 $g/m^2$ to

280-290 g/m$^2$ from Year 1 to Year 2. The detected litter scores in the second year are in line with former findings where litter scores up to 700 g/m$^2$ were found in abandoned and sown fields (Touzard et al. 2002; Foster et al. 2007). The litter accumulation detected in our study was probably caused by the increased graminoid phytomass production of sown grasses, but further, long-term monitoring of changes after restoration is necessary to explore sophisticated details of the processes in phytomass changes (Virágh et al. 2008). We found a strong negative correlation between litter and forbs (both phytomass and richness). These results support the findings of Eckstein & Donath (2005), where suppressive effect of litter was confirmed in recovered grassland, if amount of litter exceeds 200g/m$^2$.

*Implications for restoration*

One of the research hypotheses was that the evenness and amount of graminoids and litter is higher in sown grasslands than in target grasslands. This was only partly supported by our findings. Much higher litter and graminoid phytomass was detected in restored fields than in target grasslands, but the evenness of both scores was similar in restored fields and target grasslands. The detected scores of litter and graminoid phytomass in Year 3 were higher than scores in target grasslands. The detected litter (Year 3: 130-466 g/m$^2$) and graminoid phytomass scores (Year 3: 701-905 g/m$^2$) were also higher than scores detected in a grassland recovery in variously aged extensively managed lucerne fields in this region (up to 165 g/m$^2$ litter and up to 253 g/m$^2$ graminoid phytomass in one to 10 year-old fields, Török et al. 2011b). This higher phytomass and litter production was probably supported by the residual surplus of soil nutrients typical after the termination of agricultural cultivation, found also in our region and other studies of grassland restoration (Pywell et al. 2002; Foster et al. 2007; Kelemen et al. 2010; Török et al. 2010). This increased level of phytomass production is beneficial for the suppression of early weedy forbs found in the present study and also suggested by others (Lepš et al. 2007). However, the increased levels of litter and graminoid phytomass can also hamper the establishment of several characteristic grassland species by (i) competitive exclusion (Foster & Tilman 2000; Anderson 2007) and/or by (ii) decreasing gap availability (Facelli & Pickett 1991; Ruprecht et al. 2010). To facilitate the development of a natural species composition typical in target target grasslands, the reduction of litter and graminoid phytomass may be necessary. Several studies suggested that the recovery of low levels of nutrients characteristic to target grasslands in restoration sites can last several decades (Knops & Tilman 2000; Foster et al. 2007). Therefore, introducing traditional levels of management characteristic to target grasslands may not be the most appropriate option to decrease

phytomass in sites with improved productivity (e.g. mowing once a year, or low intensity grazing, Török et al. 2010). Reintroduction of the traditional management with increased frequency and/or intensity can be the proper management option (e.g. mown twice a year, high intensity grazing by cattle and/or sheep). However, it may suitable if only low intensity management is applied in the first several years because of the seed bank weeds (Renne & Tracy 2007).

# General conclusions

In the dissertation the success of grassland recovery using spontaneous succession and technical reclamation in various grasslands types was assessed. First, the restoration potential of local seed banks in the restoration of abandoned fen- and dry-mesophilous hay-making meadows was evaluated. Second, the spontaneous recovery of loess grasslands on extensively managed lucerne fields was studied. Third, the applicability of alkali and loess grassland restoration by sowing low diversity seed mixtures on former lucerne fields was studied. Finally, the role of litter and graminoid biomass accumulation on species richness and biomass of early colonising forbs in former lucerne fields sown with low-diversity seed mixtures was evaluated.

In abandoned hay meadows we found that the recovery of former species richness cannot be based exclusively on the local seed banks using resumed management. Regardless the vegetation type only a small number of target species and hardly any protected species build up detectable seed banks. Consequently, these species become extinct locally when they disappear from the above-ground vegetation. Our results demonstrate that even closely positioned stands of dry-mesophilous and fen meadows require distinct restoration measures. In spite of similar site conditions and vegetation, the density and species composition of seed banks in the two meadow types are different. In fen meadows one can rely on a spontaneous recovery of relatively species-rich stands applying the former management. Regeneration of dominant grasses, sedges and several common forbs from local seed banks is promising in fen meadows. Poorly developed seed banks of dry-mesophilous meadows do not guarantee the regeneration of species-rich vegetation. Thus, introduction of propagules is a further requirement for dry-mesophilous meadows (e.g. hay transfer from remaining species-rich stands). Our results stress the importance of regular management for species-rich hay meadows, as the most economic way of conservation. These stands can also serve as donor sites for improving degraded ones.

We found in abandoned lucerne fields that spontaneous recovery of basic grassland vegetation is promising, which offers an effective solution from the economic (agricultural) and conservation management point of view. We conclude that spontaneous recovery of grasslands should be increasingly integrated in ecological restoration. Our results suggest that the recovery of initial loess grasslands in former lucerne fields may not require technical reclamation (by sowing of competitor grasses and/or forbs) where nearby grasslands provide propagule sources. We found that during spontaneous succession facilitated by regular

mowing, lucerne fields were transformed into grasslands dominated by native perennial grasses within a decade. However, most of the characteristic forbs of loess grasslands were missing. Our results suggest that sowing lucerne in abandoned fields followed by extensive management by regular mowing can combine the advantages of both spontaneous succession and technical reclamation in grassland restoration. The method has several advantages over technical reclamation. In particular, there is no weed dominated stage and no intensive litter accumulation. Lucerne gradually decreases in abundance once re-sowing and/or fertilizing stops so there might be a lower microsite limitation rate compared to technical reclamation sites where competitor grasses are sown. Finally, spontaneous succession is cheaper than technical reclamation, and provides a high value hay harvest in the first few years in lucerne fields. However, futher case studies are needed to explore in which other communities and circumstances could restoration actions be based exclusively on spontaneous regeneration.

We found that grassland restoration on former lucerne fields can be accelerated by technical reclamation. Our results suggest that sowing seeds of a few competitive grass species can be a useful conservation tool to restore grasslands following the abandonment of crop production. Vegetation dominated by perennial grasses developed rather quickly, in three years, which was more rapid than in case of spontaneous regeneration of former croplands reported in other studies. Our results suggested that sowing low diversity seed mixtures is an effective tool to eliminate early weed dominance typical after ploughing up. The cover and biomass of short-lived weeds decreased significantly after sowing. However, the perennial weed *Elymus repens* established in the restored fields which can hamper the success of grassland restoration. It can be concluded that sowing low diversity seed mixtures can speed up the restoration of species-poor grasslands with grass dominated physiognomy (e.g. alkali grasslands), but for the restoration of species-rich grasslands, further management is needed.

We detected an increased amount of graminoid phytomass and litter in restored fields compared to these scores in the reference grasslands, which is beneficial for the suppression of short-lived weedy forbs. This higher phytomass and litter production was probably supported by the residual surplus of soil nutrients typical after the termination of agricultural cultivation. We found that the increased levels of litter and graminoid phytomass can hamper the establishment of several characteristic grassland species by competitive exclusion and/or by decreasing the availability of suitable microsites. To facilitate the development of a natural species composition typical in targeted seminatural grasslands, the reduction of litter and graminoid phytomass may be necessary.

It can be concluded, that spontaneous succession and sowing low diversity seed mixtures in former lucerne fields proved to be effective in the restoration of species-poor grasslands dominated by grasses (e.g. alkali grasslands). We found that the full recovery of species richness in restored grasslands requires more time and/or should be facilitated by direct introduction of propagules of several target species. The transfer of hay, low intensity grazing or continued mowing can be options to facilitate the establishment of target species. Traditional mowing regimes in the restored fields and the transfer of hay from natural grasslands introduce effectively the target species in the restored fields and eliminate the negative effects of limited spontaneous dispersal. We can also directly introduce the propagules of target species by sowing. Traditional grazing by sheep or cattle can transfer propagules of the target species and can enhance their establishment in the restored fields creating gaps. If grazing starts in the morning in seminatural grasslands and continues in the restored grasslands thereafter, livestock can facilitate the immigration of propagules in their gut or attached to their fur.

# Implications for practice

### Restoration measures

The usefulness of the studied restoration techniques depends on the site conditions, history, availability of donor sites and propagule sources. The budget and time available for restoration actions are also crucial points. It is advisable for further studies to report detailed information about the implementation of restoration actions and make conclusions about the restoration success.

The first study (Chapter 1) demonstrated that the complete restoration of former species richness of hay meadows is not possible by reintroducing the traditional management. This is especially true for dry-mesophilous meadows, where low propagule densities in the soil suggest poor restoration prospects. Besides regular management by mowing and raking, species poor stands of both fen and dry-mesophilous meadows should rely at least partially on hay or propagule transfer from species-rich stands to increase diversity. Therefore, traditionally managed species-rich meadow stands of the region should have conservation priority as potential donor sites. The presence of appropriate dispersal agents (herbivores, mowing machinery) is also important to enhance the colonisation success of target species.

In the second study (Chapter 2) we found that spontaneous succession can be an option which requires low technical reclamation and very little financial investment during the restoration of grasslands in former lucerne fields. It is recommended in restoration projects aiming at no rapid results (grassland vegetation within several years) in areas with high propagule availability. If the natural processes are too slow and hindered by low propagule availability, a direct restoration intervention is recommended. The restoration of species-rich grasslands will require more active management such as propagule transfer by hay and/or moderate grazing to encourage the return of native forbs.

The results of the third and fourth study (Chapters 3 and 4) show that the use of low-diversity seed mixtures is recommended to recover grassland vegetation on a relatively large area in a short time (e.g. to heal landscape scars or prevent erosion). To fulfil this aim the introduction of rare species has only minor importance compared to the recovery of vegetation cover at the first stage. In the application of seed mixtures is necessary to use seeds of local provenance to avoid establishment failure by not appropriate ecotype or genetic incompatibility. A sowing density up to

a maximum of 40kg/ha is recommended to avoid extremely high competition and this density is reasonable if cost-effectiveness is taken into account. To enhance biodiversity, we can combine the two types of seed sowing methods: in a large area, we sow low-diversity mixtures (e.g. in a density of 20-25kg/ha or lower to allow the spontaneous immigration of target species), but in small scattered patches, we sow high-diversity mixtures (e.g. up to a density of 40kg/ha) to establish species rich sites. From these species rich patches further species can disperse into the low diversity mixtures sown parts facilitated by mowing or grazing.

**Guidelines for planning restoration actions**

- Know the area, soil type, and former use of the site subjected to grassland restoration and consult with regional experts for suggestions which type of grassland vegetation should be restored.

- Choose the proper restoration method in accordance with your financial background, manpower and other investments needed.

- Before a restoration action please see for subsidies to cover at least partly restoration costs. Plan also a post-restoration management proper for the selected target grassland type (e.g. mowing or grazing).

- Document every detail of your project as a reference for further actions (e.g. in case of sowing the composition and density of seed mixture, origin of the mixture, sowing procedure).

- Monitor the changes after restoration and evaluate the success.

- Make your results available for conservationists as well as for the public.

# Acknowledgements

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# Appendices

**Appendix 1.1.** Vegetation and seed bank characteristics of the meadow stands (mean±SE). Vegetation characteristics were calculated for 4m$^2$ sized plots ($n$=5 in each stand). Number of seedlings scores were calculated for seeds/m$^2$ density ($n$=5 for each stand).

| | Fen meadow stands | | | | Dry-mesophilous meadow stands | | | |
|---|---|---|---|---|---|---|---|---|
| | mown I | mown II | abandoned I | abandoned II | mown I | mown II | abandoned I | abandoned II |
| **Vegetation** | | | | | | | | |
| Species richness | 50.0±1.8 | 53.0±1.4 | 31.4±4.1 | 49.4±3.9 | 59.8±2.0 | 62.2±1.2 | 42.0±3.5 | 53.2±1.4 |
| Forb species richness | 32.6±1.1 | 38.4±1.1 | 25.4±3.4 | 35.6±2.8 | 47.0±2.1 | 48.4±0.9 | 33.0±2.9 | 41.2±1.7 |
| Flowering species richness | 30.6±1.5 | 37.0±1.8 | 12.8±2.7 | 34.6±3.0 | 23.0±1.6 | 24.0±1.4 | 16.0±2.3 | 26.4±2.2 |
| Flowering forb species richness | 17.2±0.7 | 25.2±1.1 | 9.0±2.1 | 22.2±1.8 | 14.2±1.2 | 14.8±0.7 | 9.8±1.7 | 18.2±2.5 |
| Number flowering shoots of forbs | 102.2±7.8 | 270.2±19.2 | 29.2±7.9 | 166.6±31.2 | 85.2±5.5 | 163.4±16.4 | 31.0±6.6 | 107.0±16.8 |
| **Seed bank** | | | | | | | | |
| Species richness | 20.0±1.3 | 27.0±2.1 | 18.2±1.2 | 27.2±1.6 | 15.2±2.8 | 14.2±1.6 | 14.6±0.7 | 15.0±1.9 |
| Forb species richness | 11.2±0.7 | 14.8±1.0 | 9.8±1.4 | 14.2±1.7 | 7.2±1.4 | 7.2±1.1 | 10.4±0.9 | 7.0±1.4 |
| Number of seedlings | 91,700±14,337 | 83,344±10,306 | 63,980±3,602 | 94,034±10,839 | 5,543±744 | 4,350±797 | 6,339±465 | 5,862±748 |
| Number of seedlings without *Juncus* | 15,968±1,701 | 16,791±1,678 | 12,334±878 | 15,862±1,701 | 5,437±758 | 4,138±816 | 6,313±449 | 5,703±705 |
| Number of forb seedlings | 11,034±1,461 | 12,573±1,360 | 8,090±984 | 9,284±1,410 | 3,474±505 | 2,466±738 | 4,907±671 | 3,342±734 |

**Appendix 3.1.** 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-m² subplots). 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-m² subplots were pooled on the plot 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 subplots 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 forbs | 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 forbs | 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 forbs | 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 forbs | 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 |