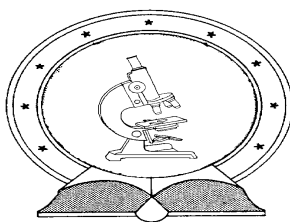


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**CONSERVING GRASSLAND BIODIVERSITY BY TRADITIONAL
MANAGEMENT, PRESCRIBED BURNING AND SEED SOWING**

**TERMÉSZETVÉDELMI KEZELÉSEK SZEREPE A GYEPEK
BIODIVERZITÁSÁNAK MEGŐRZÉSÉBEN –HAGYOMÁNYOS KEZELÉS,
KONTROLLÁLT ÉGETÉS ÉS MAGVETÉS**

Egyetemi doktori (PhD) értekezés

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Tanúsítom, hogy **Deák Balázs** doktorjelölt 2003-2006 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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A doktori értekezés betétlapja

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TERMÉSZETVÉDELMI KEZELÉSEK SZEREPE A GYEPEK BIODIVERZITÁSÁNAK MEGŐRZÉSÉBEN –HAGYOMÁNYOS KEZELÉS, KONTROLLÁLT ÉGETÉS ÉS MAGVETÉS

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General introduction

Grasslands are of crucial importance in biodiversity conservation and vital elements of the historical landscape of Europe (Bakker & Berendse 1999, Pullin et al. 2009). Many of the preserved grasslands stands are now protected at the national and European Union level, and this legal protection contributes considerably to their conservation success. The best practice for sustaining the desired nature conservation status of grasslands is the use of traditional management by grazing and/or mowing or including alternative management practices by burning. Traditional management is supported by governmental (horizontal and zonal Agri-Environmental Schemes) and further European Union-funded subsidies connected to the Natura 2000 system. The aims of the Natura 2000 network are (i) to protect vulnerable habitats and threatened populations of respective species and (ii) to ensure that the habitats are preserved in a desirable conservation status.

Despite the conservation efforts done so far, the extension and species richness of grasslands have been in constant decline in many parts of Europe in the past decades (Pullin et al. 2009, Török et al. 2011a). Still existing grasslands are threatened by the cessation of traditional management regimes (Kahmen et al. 2002, Poschlod et al. 2005). The cessation of traditional management can lead to (i) the accumulation of litter (Ryser et al. 1995); (ii) the encroachment of herbaceous competitors (Kahmen et al. 2002, Köhler et al. 2005) and/or (iii) woody species (Hansson & Fogelfors 2000), resulting in the decline of target grassland species in the long run (Isselstein et al. 2005).

Conservation priorities are generally outweighed by economical constraints in cases when traditional management by grazing and mowing is not cost-effective (Liira et al. 2009). On one hand, traditional grazing and mowing are no more sustainable in many regions because of the significant decrease of livestock numbers and a reduced need for forage (Isselstein et al. 2005). On the other hand, grazing and mowing can have relatively high costs in grasslands with difficult accessibility or located far from settlements (Köhler et al. 2005, Liira et al. 2009, Valkó et al. 2012). Thus, conservation managers and scientists are seeking for less costly and less labour-intensive substitutive approaches which can also maintain grassland species richness and eliminate the negative consequences of abandonment (Köhler et al. 2005, Liira et al. 2009). Carefully designed prescribed burning offers a vital solution and an appropriate and cost-effective substitution to grazing and mowing (Page & Goldammer 2004, Valkó et al. 2012).

Despite the legal protection and appropriate management of priority grassland habitats of the Natura2000 network, there is an urgent need for the

preservation or restoration of the original landscape structure. In many regions of Europe only small grassland fragments have remained, which are isolated by intensively cultivated agricultural lands (Öster et al. 2009). Beyond the effects of fragmentation, the general intensification of agriculture in the landscape further threatens the biodiversity of grassland fragments. To preserve these fragments and their biodiversity and to re-establish connections between them, the restoration of grasslands on former croplands is a high priority of nature conservation (Walker et al. 2004; Stadler et al. 2007).

In contrast with agricultural intensification, large-scale abandonment of low-productivity agricultural areas is common in certain parts of Europe and the world (Cramer et al. 2008). The rate of abandonment of croplands depends on socio-economic factors and differs greatly from the west to the east in Europe (Ramankutty & Foley 1999). In Western Europe, subsidy systems established under the Common Agricultural Policy have led to increased agricultural activity, further intensification and the reuse of fallows. In Central- and Eastern Europe, the collapse of socialist regimes resulted in the collapse of state-owned agricultural cooperatives and led to the privatization of land in the early 1990's (Török et al. 2011a). Land was often privatized to their previous owners of advanced age or to farmers who could not cultivate it due to their insufficient financial background. Competition from imported agricultural goods produced by farmers heavily subsidized in Western Europe further decreased the intensity of agricultural cultivation and accelerated the rate of land abandonment (Pullin et al. 2009). For example, 600 000 hectares or 10% of all croplands have been abandoned between 1990 and 2004 in Hungary, and the rate of abandonment was similar (10-20%) in four other Central and Eastern Europe countries (Cramer & Hobbs 2007).

The restoration of grasslands on abandoned croplands offers a great opportunity to mitigate or stop processes which damage grassland biodiversity (Stevenson et al. 1995, Hayward 2009). Thus, grassland restoration on abandoned croplands is one of the most frequently applied habitat restoration actions in Europe (Cramer & Hobbs 2007). For example, a recent search of a database (<http://ec.europa.eu/environment/life/project/Projects/index.cfm>) containing information on LIFE projects funded by the European Union between 1992 and 2009 using the word 'restoration', and filtering to 'natural and semi-natural grassland formations' returns 290 projects (Török et al. 2011a).

The major goals in such grassland restoration 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). Grassland restoration in former arable lands offers an opportunity to mitigate the overall loss of grassland biodiversity (Ewers & Didham 2005; Römermann et al.

2005; Plieninger & Gaertner 2011). Grassland restoration can be used to establish novel grassland stands, increase the area of grassland fragments, and to create connections between and buffer zones around grassland fragments (Critchley et al. 2006). Thus, negative impacts of surrounding agricultural lands (like infiltration or runoff of chemicals, mineral fertilisers and other forms of human disturbance) can be reduced (Karlík & Poschlod 2009; Török et al. 2010). To meet these goals, it is often necessary to control the biomass production in recovered grasslands preserved by different management techniques (Házi et al. 2011). Thus, the study of dry matter production in native and restored grasslands has become an important research topic in restoration ecology (Bischoff et al. 2005; Guo 2007).

The relation of total aboveground biomass to species richness can be often described by a hump-shaped curve where a negative correlation can be observed if high biomass scores are reached (Grime 1979; Oomes 1992; Guo 2007; Kelemen et al. 2012). Old-fields and restored grasslands can be characterised typically by high biomass production (Carson & Barrett 1988) because of the high residual nutrient content regularly occurring following the former agricultural activity (Huston 1999; Csecserits et al. 2011). In turn, high biomass production often results in a high rate of litter accumulation (Odum 1960).

Litter and graminoid biomass play a crucial role in grassland dynamics (Martin & Wilsey 2006). Accumulated graminoid biomass and litter usually hamper germination (Foster & Gross 1998) by reducing the irradiance of the soil surface (Foster & Gross 1997), forming a physical barrier (Wedin & Tilman 1993) or by altering the competitive environment (Kotorova & Lepš 1999; Rotundo & Aguiar 2005). Dense litter layer decreases the average soil temperature and reduces the variability of temperature by mitigating extremities (Eckstein & Donath 2005), which results in the decrease of 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 biomass and litter may suppress the early colonising weedy forbs that are abundant after abandonment.

Weed control can be a major benefit of restoration, especially in areas such as abandoned croplands, roadsides, and field margins (Blumenthal et al. 2005). Weed control is becoming increasingly important because of the recent high rate of abandonment of agricultural lands in Central and Eastern Europe, and likely elsewhere (Cramer et al. 2008; Pullin et al. 2009). It is often a high priority to

control weeds in abandoned areas to avoid weed infestation of natural habitats and agricultural fields and to slow their spread in the landscape (Blumenthal et al. 2003). Given the generally high cost of weed control, the potential benefit of grassland restoration can be a powerful argument to convince decision makers to fund grassland restoration actions worldwide.

Agricultural weed species as ‘ruderal strategists’ are generally characterised by high growth rates, short life span and high reproductive allocation in the form of plenty of persistent seeds (Bekker et al. 1997; Thompson et al. 1997). Weeds can rapidly establish in abandoned croplands already having vegetative propagule banks (e.g. tillers or rhizomes) and/or seed banks in the soil (Grime 1979; Prach et al. 2007). Weeds are often successful competitors in crop fields where high levels of soil nutrients are available but usually poorly adapted to late successional competitive environments (Blumenthal et al. 2005; Török et al. 2008). This observation raises the possibility that restoration using a direct sowing of late successional competitor species may be useful in weed control. Although grassland restoration by seed sowing is often recommended, especially in sites where weed domination is foreseen (Prach & Hobbs 2008; Hedberg & Kotowski 2010), the effectiveness of sowing in weed suppression was analysed only in a few studies (e.g. Van der Putten et al. 2000; Lepš et al. 2007).

The present dissertation discusses several perspectives and aspects of the management and restoration of European grasslands, focusing on alkali grasslands. In Habitats Directive (Council Directive 92/43/EEC on the Conservation of natural habitats and of wild fauna and flora) which is a cornerstone of Europe's nature conservation policy, alkali grasslands “Pannonic salt steppes and salt marshes (1530)” are included as a priority habitat type. Pannonic salt steppes and salt marshes are one of the best preserved grassland habitat types in Europe typical for the Pannonian bio-geographical region and more than 99% of their remained natural stands are located in Hungary. They are present at sites with special soil (high salt content, high groundwater level) and climatic conditions (continental climate). Alkali grasslands are used as extensively managed pastures, because their poor soil quality and fluctuating water regime are unsuitable for intensive agriculture and forestry. Their unique flora and fauna is well preserved till now and these habitats harbour rare plant and animal species. Many of them are listed in Annex I and Annex II like *Cirsium brachycephalum*, *Acrocephalus paludicola* and *Gortyna borelii lunata*.

Aims of the study

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

Chapter 1. In this chapter we aimed at to discuss the most important alkali grassland types, their traditional management, current conservation status, and restoration possibilities.

Chapter 2. In a critical review we evaluated the results of the European attempts to use burning in grassland conservation, and assessed whether or not the targeted objectives were achieved. We discussed burning studies from North-America to identify which findings can be adapted to the European grassland conservation strategy with a special emphasis on grassland biodiversity.

Chapter 3. We provide here a review of the frequently used restoration techniques (spontaneous succession, sowing seed mixtures, transfer of plant material, topsoil removal and transfer), and techniques used to improve species richness (planting, grazing and mowing) to recover natural-like grasslands from ex-arable lands, focusing on their usefulness to restore biodiversity and their practical feasibility and costs.

Chapter 4. Our aim was to test the usefulness of sowing low-diversity seed mixtures followed by annual mowing, a frequently used restoration technique, in weed suppression. We studied the effects of litter and biomass of sown grasses on species richness and biomass of early colonising forbs in former alfalfa fields sown with low-diversity seed mixtures in Hortobágy National Park. Here we measured both species richness and biomass of litter, forbs, and sown grasses. We also studied the short-term vegetation dynamics and soil seed banks of restored grasslands on former croplands in the first three years after seed sowing.

Chapter 1

Conservation and management of alkali grasslands

Summary

Grasslands are vital landscape elements in Europe; the 180 million hectares of grasslands have a crucial role in maintaining the landscape level biodiversity. Alkali grasslands are typical in Central- and Eastern Europe, with large areas in the Carpathian-basin. These types of grasslands were not the most favorable targets of arable farming, but large areas affected by mineral fertilization, drainage, soil melioration and/or commercial seeding in the last 60 years. In our paper we present important vegetation characteristics, species composition and management of five grassland types from the open annual alkali pioneer swards to tall grasses dominated wet alkali meadows. In general, alkali grasslands are usually characterized by short (*Festuca pseudovina*, *F. rupicola*, *Poa angustifolia*) or tall grasses (*Alopecurus pratensis*, *Agropyron repens*). They harbor several steppe endemics (e.g. *Plantago schwarzenbergiana*, *Cirsium brachycephalum*, *Limonium gmelinii* ssp. *hungarica*, *Puccinellia limosa* and *P. peisonis*) and halophyte species (*Salicornia prostrata*, *Salsola soda*, *Suaeda pannonica*, *S. maritima*), adapted to high salt contents of soil. According to the uneven pattern of soil salt and water, alkali grasslands are spatially very diverse. Maintaining alkali grasslands the extensive grazing mostly by cattle and sheep is essential. Nowadays, in large areas of alkali grasslands former grazing are ceased or replaced with mowing. This resulted in a change of species composition, decreased richness and/or litter accumulation. Alkali grasslands are refugees of alkali steppe vegetation; thus, restoration and preservation of their biodiversity have a high conservation priority in Habitats Directive of the EU (Pannonic salt steppes and salt marshes, 1530).

Aims of the study

In this study we focus on the restoration and management of alkali grasslands a priority habitat type of the Natura 2000 network (Pannonic salt steppes and salt marshes, 1530). First we provide a brief description of the specific environmental conditions on which these grasslands are formed. Second, we introduce the most important types of alkali grasslands and their species composition. Third, we give an overview of the traditional and current management status of alkali grasslands.

Finally we discuss the restoration possibilities of this habitat type and list the most relevant Hungarian restoration projects related to this topic.

Soil conditions and climate

Continental alkali grasslands are influenced by the high soil salt content and dynamic changes of water regime. These types of grasslands are generally located in soils with high levels of groundwater and at least moderate salt concentration (Na_2CO_3 , NaCl , rarely K_2CO_3 and KCl) and a high pH (8-10) under a continental climate. The soil salt content is originated from eroded debris transported by groundwater from volcanic mountains and sodium, calcium and magnesium content of the bedrock (predominantly loess). Due to the intensive evaporation caused by often extreme, dry and warm summer periods, the groundwater which is near to the soil surface and have high salt content transports the salt to the upper soil layers where its accumulates.

Types of alkali soils and grasslands are generally determined by the vertical position of salt accumulation zone and groundwater level. The least productive types are where the groundwater level is high and the salt accumulation zone is at or near to the soil surface. Characteristic alkali soil types are solonchak and various types of solonetz. *Solonchak* soils frequently have a considerable sand soil fraction and are characterized by high mean groundwater levels where the salt accumulation zone is near located to the soil surface. The humus content is generally low. There is generally no definite geometric soil structure. *Solonetz* soils are well structured and can be characterized with deeper groundwater tables and salt accumulation zones than solonchak soils. The steppic types are characterized by high humus content. The upper soil layer can be very hard (when dry) or soapy (when wet).

Alkali soils develop by natural or a human induced way (Molnár & Borhidi 2003). Naturally developed alkali soils are present in the Carpathian-basin since the Pleistocene with considerable extent (Bárczi et al. 2006). Secondary alkali soils are formed after drainage or river regulation works, which was typical from the 19th century (river regulations) till the end of the socialist era (irrigation in marshes and fens) in the Carpathian basin. The lowered water levels and desiccation of habitats induced secondary salt accumulation in higher soil layers especially in former wet non-alkali meadows, marshes or even in fens (Molnár & Borhidi 2003).

Grassland types

Alkali grasslands are typical in regions with at least moderately continental climate, extent stands located from Middle-Asia (e.g. Siberia and Mongolia) to Middle- and Eastern-Europe (Ukraine, Romania, Hungary), but very sporadic in Western Europe. The largest native occurrence of alkali grasslands to the west is located in the Carpathian-basin (mostly in Hungary and Romania, but some minor grassland patches are present in Austria, Slovakia and in the Czech Republic).

The dominant species of most alkali grassland types are widely distributed grass species with a wide range of humidity- and salt tolerance (*Agropyron repens*, *Agrostis stolonifera*, *Alopecurus pratensis*, *Beckmannia eruciformis*, *Festuca pseudovina* and *F. rupicola*). Alkali grasslands harbor several grassland species characteristic to Eurasian continental steppes and several endemics to the Carpathian basin. Several alkali grassland types harbor the same common grassland species; thus their classification is based not only on differential species and species composition but on the relative proportion of dominant species. On habitats with extremely high salt contents and rapid changes in water availability sparse halophytes dominated vegetation is typical. These types of grasslands are classified in “Annual alkali pioneer swards of steppes and lakes” when several short lived herbs are characteristic, and in “Dense and tall *Puccinellia* swards” if *Puccinellia* spp. are present with a relatively high abundance. The relatively dry, short-grass alkali grassland types are “*Artemisia* alkali steppes” and “*Achillea* alkali steppes” on meadow solonetz or solonchak. Both types are characterized by the same short grasses, but the latter one generally harbors several non alkali species (species characteristic to loess grasslands). Tall grasses dominated species-poor meadows on alkali soils are classified into the “Alkali meadows” type. The “Tall herb alkali meadows and meadow steppes” harbor the same tall grass species as the former type, but are generally situated on higher elevations with higher richness of forbs characteristic for loess grasslands, alkali steppes and alkali meadows. In the followings we present these types of alkali grasslands in the Carpathian basin, in accordance with the classification of Molnár et al. (2008).

Extent homogeneous stands of a single alkali grassland type can be rarely found; various types of grasslands form generally a heterogeneous mosaic structure in accordance with the uneven pattern of soil salt contents, relief and water availability. In a landscape characterized by alkali grasslands near to the highest elevated plateaus and point bars with loess vegetation generally stands of *Achillea* alkali steppes are situated. Near to *Achillea* alkali steppes but at lower elevations on soils with higher salt content (solonetz or solonchak) typically *Artemisia* alkali steppe vegetation is located (Molnár & Botta-Dukát 1998; Török et al. 2011b). At

the lowest elevations alkali meadows, while in the deepest depressions alkali marshes are situated.

Annual alkali pioneer swards of steppes and lakes

These types of habitats are typical on salt lake beds and several micro-formations of alkali landscape characterized by extremely high salt accumulation at or near to the soil surface, low soil fertility and high groundwater level even in summertime. Annual alkali pioneer swards of steppes and lakes have a low vegetation cover and harbor a high number of endemic (*Puccinellia peisonis*, *Suaeda pannonica*, *S. salinaria*) and common halophyte species (*Camphorosma annua*, *Lepidium cartilagineum*, *Matricaria recutita*, *Plantago maritima*, *Salicornia prostrata*, *Spergularia maritima*, *Suaeda maritima*).

Dense and tall Puccinellia swards

They are generally wet and species poor alkali habitats with high concentration of accumulated salt in the upper soil layers. Their stands are covered with shallow water in the spring. The vegetation cover usually exceeds 50% in springtime, but in dry years and/or seasons this cover can decrease to a few percent. Stands are more typically located in solonchak soils where the extension of continuous stands reaches several hectares. Most characteristic are the endemic *Puccinellia* species (*Puccinellia limosa*, *P. pannonica* and *P. peisonis*), and the commonly widespread *P. distans*, however the vegetation composition changes very dynamically in time. In wet years several *Juncus* species and *Alopecurus pratensis* can reach considerable cover. In dry years short-lived forbs like *Artemisia santonicum*, *Camphorosma annua*, *Cerastium dubium*, *Matricaria recutita*, *Pholiurus pannonicus*, *Plantago maritima* and *P. tenuiflora* become frequent. *Puccinellia* swards are generally used as pastures grazed by cattle.

Artemisia alkali steppes

Artemisia alkali steppes are characterized by short grasses (mainly *F. pseudovina*) and two subspecies of *Artemisia santonicum* (*A. santonicum* ssp. *santonicum* and *patens*; the latter is an endemic subspecies) regularly used as pastures. These grassland types are generally covered by shallow water (a few mm) in springtime. Polygonal soil splits may appear on the soil surface in the dry summer. *Bupleurum tenuissimum*, *Cerastium dubium*, *Gypsophila muralis*, *Limonium gmelinii* ssp. *hungarica*, *Lotus tenuis*, *Podospermum canum*, *Ranunculus*

pedatus and several *Trifolium* species are frequent species of alkali steppes. Salt tolerant species like *Aster tripolium* ssp. *pannonicum*, *Atriplex littoralis*, *Lepidium cartilagineum*, *Plantago maritima*, *Suaeda* spp. are widespread.

Artemisia alkali steppes have several endemic species like *Aster tripolium* ssp. *pannonicum*, *Limonium gmelinii* ssp. *hungarica*, *Suaeda* spp., *Puccinellia* spp. and *Plantago schwarzenbergiana* which is present in disturbed stands. If suitable water conditions are met (e.g. in springtime) and overgrazing occur several short-lived species (*Erophila verna*, *Hordeum hystris*, *Matricaria recutita* and *Polygonum aviculare*) are present. In wet years in open patches several species characteristic to annual alkali pioneer swards (*Myosurus minimus*, *Puccinellia limosa*, *Scleranthus annuus*) occur.

Achillea alkali steppes on meadow solonetz

Achillea alkali steppes are closed, short-grass steppes on solonetz soils with a moderate salt contents (meadow and chernozem solonetz), characterized by short grasses (*Festuca pseudovina*, *F. rupicola*, *Koeleria cristata*, *Poa angustifolia* and in heavily grazed stands *Cynodon dactylon*). Considerable stands of *Achillea* steppes were originated due to secondary salt accumulation. Several species characteristic also for loess grasslands are common (*Dianthus pontederiae*, *Filipendula vulgaris*, *Silene viscosa*, *Salvia austriaca*). Because of the relatively low soil salt concentration only a few halophyte species are characteristic in these grasslands. *Achillea* steppes are rich in forb species, the most frequent species are *Achillea collina*, *A. setacea*, *Bupleurum tenuissimum*, *Cerastium dubium*, *Gypsophila muralis*, *Inula britannica*, *Plantago lanceolata*, *Podospermum canum*, *Ornithogalum kochii*. Several *Trifolium* species are also present (*Trifolium angulatum*, *T. fragiferum*, *T. retusum*, *T. striatum*, *T. strictum*). These types of grasslands are traditionally used as pastures grazed by cattle or sheep. In overgrazed stands grazing tolerant species can appear (*Carduus nutans*, *Cynodon dactylon*, *Eryngium campestre*, *Ononis spinosa*).

Alkali meadows

Alkali meadows are tall grasslands dominated by tall grasses like *Alopecurus pratensis*, *Agrostis stolonifera*, *Agropyron repens*, *Beckmannia eruciformis*, and *Glyceria fluitans*. This type of alkali grassland is generally covered by shallow water from early spring till midsummer. There are usually two herb layers. In the upper herb layer with the tall grasses several tall forbs are characteristic (e.g. *Lycopus europaeus*, *Lythrum salicaria*, *L. virgatum* and *Rumex stenophyllus*). In the second

herb layer small forbs (*Cerastium dubium*, *Galium palustre*, *Inula britannica*, *Leonurus marrubiastrum*, *Lotus tenuis*, *Lysimachia nummularia*, *Mentha aquatica*, *M. pulegium*, *Oenanthe silaifolia*, *Ranunculus lateriflorus*, *R. repens*, *R. sardous*) short sedges (*Carex distans*, *C. melanostachya*) and rushes (*Juncus compressus*, *J. gerardii*) are present. Two endemic species *Rorippa sylvestris* ssp. *kernerii* and *Cirsium brachycephalum* are typical in most stands. These grasslands are traditionally extensively grazed or used as hay meadows.

Tall herb alkali meadows and meadow steppes

Originally these grasslands are typical in the clearings of alkali steppe oak woodlands (Bölöni et al. 2008, Molnár et al. 2008). The vegetation of these tall alkali grasslands are characterized by several tall grasses and herbs. In springtime they are usually wet, and they get dry till late summer. Characteristic species are tall grasses as *Alopecurus pratensis* and *Agropyron repens* and several tall forbs like *Aster sedifolius*, *Rumex pseudonatronatus* and *Peucedanum officinale*. Several species of loess steppes (*Falcaria vulgaris*, *Fragaria viridis*, *Galium verum*, *Peucedanum alsaticum*, *Stellaria graminea*) and several salt tolerant species (*Artemisia pontica*, *A. santonicum* and *Limonium gmelinii* ssp. *hungarica*) occur. This habitat type is rare and of high conservation value in the Carpathian basin and traditionally managed by low intensity cattle grazing.

Management and threats

Traditional management

Alkali grasslands were maintained by the large wild herbivores from the Pleistocene till the early Holocene (Bárczi et al. 2006). Parallel to the increase of the human presence in the Carpathian-basin these herbivores have disappeared. Their role was taken over by domestic grazers like cattle, sheep and horse. Nomadic herding in alkali habitats was present from the middle ages till the end of the Second World War.

Artemisia and *Achillea* alkali steppes, *Puccinellia* swards and annual alkali swards of steppes were generally used as pastures for sheep. Cattle grazing is typical on all alkali grassland types, but is more frequent on *Achillea* and *Artemisia* alkali steppes and alkali meadows. Wet meadows and marshes were also grazed by Hungarian Grey cattle and Water Buffalo. The optimal stocking density was one large livestock (cattle, horse or buffalo) or 4-7 sheep per hectare. Traditionally only

a negligible part of the meadows were mown for producing some additional winter forage.

Traditionally, the most suitable time for mowing was at the beginning of flowering of the frequent grass species, usually in May. In some years the mowing time could have an overlap with the breeding time of several protected bird species, or in wet years the soil surface can be covered by water. Thus; in practice, mowing of nature conservation areas is only permitted from the middle of June, but only with mowing machinery equipped with an instrument warning nesting birds (e.g. chains attached to the front of the mower).

Current management and threats

From the middle of the 20th century onwards the number of livestock decreased rapidly because of the economic and political changes after the Second World War. At the early years of the socialist era several attempts were made to improve the poor fertility of pastures by draining water, melioration, use of fertilizers, commercial seeding and by application of pesticides. The former use by nomadic herding was in several places replaced by intensive animal farming where the livestock was kept in stables. An additional effect of the established animal farming systems was, the increased rate of linear infrastructures (e.g. roads and canals) was necessary to transport additional forage and take away animal dung.

To provide forage for stabled livestock most of the formerly grazed alkali meadows were transformed to hay meadows. The mowing by mowing machinery resulted in a more homogeneous vegetation structure than grazing and this change in land use altered the species composition of the meadows (Török et al. 2011b). The former patch dynamics were destroyed and several species adapted to grazing-induced patchiness (e.g. characteristic short-lived endemics adapted to regular trampling and grazing) became rare.

It was also typical, that in several pastures livestock grazing was replaced by grazing of domestic geese. Ten thousands of domestic geese were fenced in a relatively small area which caused a dramatic decrease in the cover of grassland species and increase that of weeds in the subjected grasslands. Thus, goose grazing is not allowed in protected Natura 2000 sites nowadays.

After large state-run agricultural co-operatives have collapsed and lands were often privatized after 1990 the cessation of former management became typical. By the cessation of management by grazing and mowing the species number, heterogeneity and number of microhabitats (formed by regular disturbance by grazing and mowing) was decreased. Abundance of frequent grassland species e.g. *Alopecurus pratensis*, *Agrostis stolonifera*, *Agropyron repens* in meadows, *Festuca*

and *Artemisia* species in short-grasslands and the amount of litter increased. These changes resulted in a decrease of plant species richness found also in other type of grasslands (Valkó et al. 2011). The formed homogenous grassland stands with high litter accumulation became also improper for birds (e.g. for *Charadrius alexandrinus*, *Glareola pratincola*, *Tringa tetanus* and *Vanellus vanellus*) preferring open grassland patches for nesting. The developed thick litter layer can prohibit the reintroduction of grazing and can increase the probability of spontaneous fires. However, it is important to stress that in lack of grazing (or mowing) no spontaneous tree and shrub invasion can be foreseen, because the environmental conditions are improper arboreal vegetation.

The increase of several invasive species was recently detected caused by unfavorable changes in hydrological and management status of alkali grasslands. Non-native invaders in dry alkali grasslands are *Eleagnus angustifolia* and *Hordeum jubatum*. In abandoned wet alkali meadows and marshes the spread of the alien *Amorpha fruticosa* was detected. Three other non-native tree species *Acer negundo*, *Ailanthus altissima* and *Fraxinus pennsylvanica* are typical invaders in riparian forests and near to water streams. Thus, their spread to alkali meadows with low soil salt contents can be foreseen.

Conservation remarks

Several recent attempts were made to restore and conserve alkali grassland biodiversity in the Carpathian basin. In one of the largest alkali habitat complex in the Hortobágy Puszta several large scale habitat restoration projects were started from 2002 onwards, funded by the EU. To restore the historical water regime of water drained marshes and grasslands the key action was to eliminate irrigation systems (dikes and channels). In the project “Restoration of pannonic steppes, marshes of Hortobágy National Park” (LIFE02NAT/H/008634) 560 km of draining channels was eliminated between 2002 and 2005 and further 400 km will be eliminated in the near future.

The largest known alkali grassland restoration in Europe was in Egyek-Pusztakócs, Hortobágy National Park, Hungary. In this project co-financed by the LIFE Nature programme and the EU (LIFE04NAT/HU/000119), altogether 665 ha of alkali grassland was restored in 2004-2008 period using low diversity seed mixtures of local provenance (for details see Török et al. 2010). To restore Important Bird Areas in alkali landscapes in the projects “Habitat management of Hortobágy eco-region for bird protection” (LIFE02 NAT/H/008638), “Sodic lake habitat restoration” (LIFENAT07 /H/000324), and “Conservation of *Otis tarda* in Hungary” (LIFE04 NAT/HU/000109) restoration of alkali steppe and wetland habitats were

planned to provide feeding and breeding habitats for endangered bird species (e.g. *Chlidonias leucopterus*, *Grus grus*, *Otis tarda*). These aims are fulfilled with complex habitat restoration measures including rewetting actions, grassland recovery by sowing of low diversity seed mixtures (over 350 ha in the Kiskunság National Park and in the Hortobágy National Park) and reintroduction of former management by extensive grazing. Due to these efforts the nesting populations of the protected bird species were increased significantly (e.g. these increase was more than 16% for *Otis tarda* populations).

Chapter 2

Critical evaluation of prescribed burning as a management tool in European grasslands

Summary

Prescribed burning is an integral part of the North-American grassland conservation practice, while in European grasslands this technique is rarely applied. European grassland managers and scientists are increasingly interested in cost-effective, alternative ways of biodiversity conservation and prescribed burning can be a vital solution to several conservation problems. Our goal was to draw attention to the use of prescribed fire as a neglected but promising management tool in European grasslands. We evaluated the results of European attempts to use burning in grassland management and we found that European studies on this topic are scarce, and mostly yearly dormant-season burning is applied. The reviewed studies concluded that yearly burning solely is not an appropriate option to preserve and maintain species-rich grasslands. Second, we discussed burning studies from North-America to identify which findings can be adapted to the European grassland conservation strategy. In North-America, contrary to Europe, the application of burning is fine tuned in terms of frequency and timing and is generally combined with other restoration measures (grazing, seed sowing or herbicide application). Thus, multiple conservation goals, like invasion control and increasing landscape-level heterogeneity can be linked. Finally, we emphasize that for the application of prescribed burning in Europe, the general findings of carefully designed case studies should be combined with the practical knowledge of conservation managers concerning the local application circumstances to reach specific management objectives.

Aims of the study

We evaluated the results of the European attempts to use burning in grassland management, and assessed whether or not the targeted objectives were achieved. We discussed burning studies from North-America to identify which findings can be adapted to the European grassland conservation strategy with a special emphasis on grassland biodiversity. Our review was compiled from a literature search of

electronic sources (ISI Web of Knowledge; JSTOR, Science Direct and Google Scholar) using the keywords 'fire' OR 'burn' AND 'grassland'. After the search, further studies were added from the reference list of the selected papers.

Prescribed burning as a management tool

Prescribed burning is the carefully designed application of fire under specified fuel and weather conditions to meet specific resource management objectives and long-term conservation management goals (Castellnou et al. 2010). Prescribed burning practices are well-developed in North-America in various ecosystems like forests (Harrod & Halpern 2009; van Mantgem et al. 2011), shrublands (Keeley 2002) and in several grassland types (Fuhlendorf & Engle 2004; Cummings et al. 2007; MacDougall & Turkington 2007). In Europe burning was successfully applied as a management tool in heathlands (Marrs et al. 2004; Måren & Vandvik 2009; Davies et al. 2010); shrublands (Baeza et al. 2002; Pons et al. 2003) and forests (Fernandes & Botelho 2003; Kuuluvainen 2009) but only in a few cases in grasslands (Page & Goldammer 2004; Rietze 2009).

There are contrasting opinions in considering burning as a management tool. One hand, burning can be used effectively with relatively low implementation costs (i) to manage open landscapes (Page & Goldammer 2004), (ii) to reduce accumulated litter (Ryser et al. 1995; Liira et al. 2009), (iii) to speed up the recovery of target grasslands in restoration (Rowe 2010) and (iv) to decrease the chance of wildfires (Baeza et al. 2002). On the other hand burning can also have serious detrimental impacts on grassland ecosystems by promoting the dominance of some problem species (e.g. some competitors or invasive species) and by damaging several endangered plant and animal species, especially invertebrates (Swengel 2001; Engstrom 2010). Inappropriate burning can result in a loss of biodiversity in the long run, thus, there is an increasing need for summarizing experimental and evidence based knowledge of application of burning in European grasslands considering general (e.g. timing, frequency and duration) and specific (e.g. types of grasslands, effects on endangered species) circumstances.

General effects of burning in grasslands

The general effects of fire on grasslands and associated species should be considered in the planning of grassland management. Assessment of fire effects are linked to various factors, like the frequency, timing and severity of burning and the affected grassland type. The general effects of fire can be categorized as (i) first-order effects (e.g. killing individuals or damaging organs, reducing litter and

increasing bare ground) and (ii) second-order effects (e.g. changing the physical environment, nutrient availability and soil seed banks; Pyke et al. 2010). Some effects may be target-effects of the management (e.g. decreasing litter layer), but attention must be paid to associated non-target effects which can be either beneficial or detrimental from a conservation point of view.

Effects of burning on grassland plants

It was found that the major traits determining the response of plants to fire are (i) life form, (ii) the presence or absence of perennating buds; (iii) the density, spatial orientation and some other characteristics of seeds (Pyke et al. 2010). First-order fire effects are the death of entire plants or several organs; but in addition fire also has several second order effects on plants through the alteration of their resources, species composition and regeneration patterns.

After fire, soil microclimate often becomes warmer and drier for several weeks or months (Tix et al. 2006), which may result in an increased microbial activity (Ojima et al. 1994). High intensity fires can lead to nutrient volatilization or runoff (Pyke et al. 2010). Conversely, low intensity fires can temporarily increase available nutrients; immediately after fire there can be a flush of available ammonium and nitrate (Neary et al. 1999). As a result, in recently burned areas both above- and below-ground biomass production increase (Dhillon & Anderson 1994; Kitchen et al. 2009).

Fire significantly affects species composition by increasing resource availability (light, nutrients) parallel with decreasing competition by the killing of some neighbours (Maret & Wilson 2005). Increased productivity in recently burned grasslands can lead to a higher grazing pressure which also alters competitive interactions (Fuhlendorf & Engle 2004).

After fire, plants either regenerate from seed banks or re-sprout (Keeley & Zedler 1978; Pyke et al. 2010). Burning is known to decrease seed bank density either by killing seeds in the upper soil layers (Blodgett et al. 2000), or by breaking the dormancy and promoting the germination of certain species (Whelan 1995). Fire generally increases the availability of microsites for seed germination and seedling establishment by reducing litter. In arid conditions litter protects seedlings from desiccation (Maret & Wilson 2005; Acosta et al. 2008), so in this case the reduction of litter by fire can decrease seedling survival.

Effects of burning on animals

First-order effects of fire on animals (death or injury) may not be detrimental for the population, if second-order fire effects increase the fitness of individuals within the population (Engstrom 2010). For example, despite of detrimental first-order effects, fire can affect birds positively, because several parasite populations, like feather mites can be reduced by silicon-dioxide in the ash after fire (Lyon et al. 2000a).

The most important reasons for animal injury or death during fire are (i) oxygen deficiency, (ii) exposure to lethal heat and (iii) toxic compounds from smoke (Engstrom 2010). Most vulnerable are animals that have limited mobility (e.g. having immobile life stages in aboveground litter or plant tissue) or surface-level nests (e.g. small rodents) made of flammable materials (Lyon et al. 2000b). The vulnerability of a species is higher in sensitive life stages, like nesting season (e.g. ground-dwelling birds; Lyon et al. 2000b) or moulting period (e.g. snakes in ecdysis; Russell et al. 1999). The detection and avoidance of fire is crucial for animals to avoid detrimental effects (Whelan 1995). Several species emigrate from burned sites when required habitat features are altered (e.g. protection from predators, food availability).

Fire has some sort of secondary effects on animals, mainly through changes in habitat structure, and food availability. Post-fire habitats often have a warmer and drier microclimate which is favourable for some species (e.g. snakes), but detrimental for others (e.g. amphibians; Russell et al. 1999). Fire may interrupt biotope availability for insects dependent on certain plant structures, like flowers or fruits (Swengel 2001). Fire often increases food availability and quality; recently burned sites are preferentially selected by grazing ungulates (Fuhlendorf & Engle 2001) because foliage of re-growing herbs and shrubs is more palatable and richer in nutrients and crude protein (Tracy & McNaughton 1997). Predators and scavengers are also attracted to burned sites because of the more abundant and more exposed food than on unburned sites (Lyon et al. 2000b).

Manipulating the effects of burning in grasslands

With prescribed burning, we can promote or hamper some of the effects of fire in accordance with specific management objectives. First-order effects can be controlled by (i) choosing proper sites for prescribed burning and (ii) manipulating the frequency, timing and magnitude of burning. At an appropriate site burning does not have a potential to cause detrimental effects to remnant populations of endangered species (MacDougall & Turkington 2007). The magnitude of burning

can be manipulated in several ways (decreasing litter by raking, fuel addition, using backfires or fire breaks, choosing appropriate weather conditions for burning) to meet specific goals (Pyke et al. 2010). For example, if the aim is to kill seeds of invasive species in the soil seed banks, slowly burning, high temperature fires are required; but if we aim only the reduction of litter layer without killing seeds, low temperature, fast burning fires are needed (Pyke et al. 2010).

Second-order fire effects can be manipulated by post-fire rehabilitation. For example, fire usually increases microsite availability which can be either positive or negative from a nature conservation point of view. If there is a risk of colonization by unwanted non-native species or propagules of native species are lacking, post-fire rehabilitation by seed sowing of target species (Moyes et al. 2005) or hay transfer from target grasslands can be recommended (Török et al. 2011a, 2012). Burning prior to direct seeding can be useful to promote seedling emergence or survival of transferred species in degraded sites; however, burning can contribute to the expansion of exotic species when they are present in the seed bank (Maret & Wilson 2005).

Differences in wildfire history of European and North-American grasslands

Fire is considered as a natural disturbance which can occur in any terrestrial ecosystem. However, the probability of fire occurrence and the frequency of natural fires which shaped historical fire patterns were driven by two major factors: climate and fuel loads (Sousa 1984). Historically, fire has and probably had a higher impact shaping grasslands in North-America than in Europe.

North-American grasslands are more fire-prone than European ones which means they are evolutionally more adapted to fire. A global simulation model pointed out that the distribution and properties of several major biomes are driven by the global fire regime (Bond et al. 2005; Bond & Keeley 2005). They found that in a World 'without fire' 51.3% of C4 grasslands would be covered by forests, whereas C3 grasslands are less dependent on fire with a 41% reduction of their area in the simulation. North-American grasslands are mainly characterized by the more fire-prone C4 grasslands, while in Europe C4 grasslands are not native, only the less fire-dependent C3 grasslands.

Another reason for the differences in fire regimes between the two continents can be that in North-America, fuel loads were more continuous than in Europe until recent times. In Europe urbanization processes (creating fire breaks by linear infrastructures and settlements) started much earlier than in North America which decreased the extension and magnitude of wildfires.

Grassland management using prescribed burning in Europe

Studies found in scientific electronic databases concerning with prescribed burning as a potential management tool in European grasslands were included in Table 1. The strict regulation of burning by law in many European countries limits the possibility of implementing prescribed burning experiments (Goldammer & Montiel 2010). From many regions (South, East and Western Europe) and grassland types (e.g. acidic grasslands, alkali grasslands, loess grasslands) scarce information was published. In uppermost of the studies dormant-season burning was applied on an annual basis with a valuable long term monitoring (up to 28 years). In most of the studies no data about pre-burn vegetation composition was given only a brief description of pre-burn vegetation. Only a few studies concern with the effect of burning on animals. Most of them are comparative studies of potential substitutive measures (e.g. burning, mulching and removal of woody plants) of traditional mowing or grazing and their emphasis is not on the application of burning. Burning was chosen because being not expensive or labour intensive compared to other management options. In the published studies, burning was not combined with any other management or post-fire rehabilitation.

The reviewed studies concluded that yearly burning solely is not an appropriate option to preserve the structure and maintain species richness of the studied grasslands. Burning led to alternative successional pathways compared to other management options (mowing, grazing or mulching). In the long run, species richness usually decreased in the burning treatment compared to grazing or mowing treatments. Burning lead to the increased dominance of competitor species, like *Brachypodium pinnatum* (Ryser et al. 1995; Kahmen et al. 2002; Köhler et al. 2005), and resulted in an untargeted species composition, likely to abandonment. The reason why burning proved to be inappropriate in these studies might be that burning was applied annually for many years, and the vegetation did not have enough time to regenerate.

Only minor and not always significant advantages of burning were indicated in the reviewed papers. Although burning did not lead to the targeted species composition, it promoted some rare or endangered species of dry limestone grasslands like *Aster amellus*, *Gentianella ciliata* or *Thesium bavarum* (Köhler et al. 2005). The elimination of litter layer and the delay of woody encroachment were also suggested as positive effects. Promising examples of the use of prescribed burning in the management of meadow-type grasslands on viniculture terraces in Germany were published by Page & Goldammer (2004) and Rietze (2009).

Key findings of North-American case studies

In North-America prescribed burning is frequently included as a management option in grassland conservation and restoration programs, which is indicated by the huge number of studies on this topic. In North-America burning is not only used as a potential substitutive tool of other management regimes, but is often combined with other restoration measures (grazing, sowing seeds, herbicide application) and the overall aim of burning is often the reintroduction of traditional disturbance regimes (MacDougall & Turkington 2007). In the following section, we summarize the experiences of North-American burning practices which could at least partly be adapted to European grasslands.

Timing of burning. In North-America both dormant- and growing-season burning are applied to achieve management goals considering the phenology of target and unwanted species (e.g. germination, seed set and dispersal). Dormant-season burning is the most effective burning type in the reduction of accumulated litter. Natural fire regimes are best simulated by growing-season mid-July burns, in the peak of lightning-season (Howe 1994). Summer fires can be appropriate if the management goal is (i) to destroy certain unwanted species in a phenological state when they are the most susceptible to fire; or (ii) to give competitive advantage to certain, e.g. early-growing species which can regenerate after fire in the autumn (Howe 1994). Given the facts that highest fire risk occurs in summer (Fuhlendorf et al. 2009) and that the highest number of plant and animal species are physiologically active in this period, summer fires can cause more detrimental effects than any other burning type.

Frequency of burning. When the aim of burning is to mimic natural disturbance regimes or to maintain grassland biodiversity, e.g. in tallgrass prairies, burning in every 2-3 years is recommended (Brockway et al. 2006; Fuhlendorf et al. 2009). This period of time resembles most to the natural wildfire regimes, and is required for the regeneration of grasslands and for the re-building of fuel loads (Rowe 2010). When the aim of burning is to control invasive species high-frequency burning in several consecutive years is needed. Repeated burning may prevent the regeneration of the invasive species from vegetative buds or seed bank, burning should be repeated till the seed bank of the invasive species is destroyed and there is no risk of local re-colonization (Alexander & D' Antonio 2003; DiTomaso et al. 2001).

Combination of grazing and burning; patch-burning. Fire and grazing interact in positive and negative feedbacks causing a shifting spatial and temporal mosaic (fire-grazing model; Fuhlendorf & Engle 2001). The core of the fire-grazing model is the preferential selection of recently burned patches by free-ranging grazers,

because of the high quality forage there. Grazers rarely choose patches with no recent fire history, which leads to litter and biomass accumulation and increased fuel loads resulting in a higher probability of wildfires there. These spatially and temporally dynamic cycles play a crucial role in shaping the landscape of fire-prone grasslands, like prairies (Allred et al. 2011). A conservation effort to mimic the above described natural disturbance regimes and to improve spatial and temporal heterogeneity of grasslands can be fulfilled by the application of patch-burning (Fuhlendorf & Engle 2001). Within a large area, burning is applied in patches, each patch is being burned periodically, e.g. once in every 3 years to leave time for grassland regeneration to the pre-fire state. This technique provides a mosaic of recently burned patches (which are preferred by grazing animals) and patches that were burned some years ago (with the highest biomass and lowest grazing pressure). Patch-burning management has several advantages compared to homogenous burning of the entire area followed by grazing. (i) The co-existence of various fire regimes in patch-burning management can maximize the number of species (Parr & Andersen 2006). (ii) The increased landscape scale heterogeneity promotes the coexistence of species with different habitat requirements. (iii) Patch-burning is beneficial also from an economical point of view, because grazing animals can freely select patches with the best forage quality. (iv) Patch-burning can be an effective tool in the suppression of large wildfires by creating heterogeneous fuel structure in the landscape, where patches with low fuel loads can act as natural fire breaks (Hobbs 1996). (v) Patch-burning can also be used to control invasive plants. A promising example of invasion control by patch-burning is the control of *Lespedeza cuneata* in the primary stage of invasion in tallgrass prairies (Cummings et al. 2007). A possible explanation for this phenomenon is that after fire, unpalatable plants allocate most of their energy to regeneration and less energy to the reproduction of defense organs or secondary metabolites (Cummings et al. 2007).

The use of burning for invasion control. Burning can be a successful management tool in invasion control when the phenology of invasive and targeted native species is different or they are differently adapted to fire (MacDougall & Turkington 2005). The timing of burning plays a crucial role in invasion control, as inappropriately timed burning can even facilitate invasion in arid and semiarid ecosystems (D'Antonio 2000; Keeley 2006). For example, *Bromus tectorum* a noxious invader of North-American grasslands produces continuous fine fuels and enhances the frequency and intensity of fires. Fires promoted by *B. tectorum* fuels do not cause damages to *B. tectorum* individuals because they are physiologically not active in that period, and the seeds have already dispersed. For the effective control of this species by fire, burning before seed maturation (several months

before the peak of wildfire period) can be the only possible solution (D'Antonio 2000). Burning can be applied to increase the effectiveness of herbicide application in invasion control, because fire removes litter and provides a better contact between the herbicide and the target (DiTomaso et al. 2006). There are promising examples of application of fire and herbicides in the control of *Taeniatherum caput-medusae* (Davies & Sheley 2011), *Lespedeza cuneata* (Cummings et al. 2007) or *Centaurea maculosa* (MacDonald et al. 2006).

Post-fire rehabilitation techniques. Post-fire rehabilitation measures are applied to improve regeneration of grassland species and mitigate unwanted effects of burning. To prevent soil erosion seeding 'sterile' or non-persistent cereal grains (nurse crop) can be applied (Keeley 2006). These non-persistent species disappear for the second post-fire year, however, after that there is a risk that non-target species will colonize the sites. A more effective way of post-fire rehabilitation is mulching or hay transfer which can reduce erosion and post-fire hydrological problems (Robichaud et al. 2000), but at the same time, propagules of target species can be introduced to the site (Kiehl et al. 2010; Török et al. 2011a).

What can be learned from North-American burning studies?

The current grassland conservation practice in Europe could and should be improved based on the burning studies from North-America in terms of (i) application circumstances (timing, frequency) and (ii) management objectives. Given the differences in the history, climate and composition of the grasslands in the two continents, the elements of North-American burning practice can only partly be adapted in Europe.

Application circumstances

In most European studies dormant-season burning is applied yearly as a substitutive management tool in grasslands (see Table 1). However, there is a need for experimental case studies concerning the possible use of summer burning in degraded European grasslands to control certain problematic species. The practice of yearly burning gives no time for grassland regeneration, and can lead to untargeted states of succession. When the aim of management is to maintain open landscapes and preserve species-rich grasslands, least frequent burning is recommended. Fire return periods can largely depend on grassland type, but at least three years may be appropriate in European grasslands given the fact that they are evolutionary less adapted to fire than North-American ones.

Management objectives

We should improve the simple burning measures generally applied in European grasslands, in terms of (i) the joint application of grazing and burning and (ii) the use of fire in invasion control and (iii) the application of post-fire rehabilitation measures. In extent grassland areas (e.g. in alkali and steppe-like grasslands of Central- and Eastern Europe) the application of patch burning management can be a feasible tool to increase landscape-scale heterogeneity. Besides, further experimental studies are necessary to test the applicability of grazing-burning interactions in the control of unpalatable or poisonous invasive plants in European grasslands. Burning has one of the lowest implementation costs among invasion control techniques (Simmons et al. 2007) and it is a more natural way than the single application of herbicides which can persist in the soil (DiTomaso 2000) and also have negative impacts on grassland species (Laufenberg et al. 2005). Burning should be integrated into the European invasion control strategy by case studies of carefully timed burnings to control certain invasive species. There are several invasive species of North-American origin, which cannot easily be controlled by burning, e.g. burning promotes *Solidago canadensis* in prairies (Simmons et al. 2007) and *Asclepias syriaca* in wet grasslands (Johnson & Knapp 1995). Conducting burning experiments on degraded grasslands highly infested by invasive species has the additional advantage that there is no risk to have detrimental effects of fire on endangered populations. When necessary, post-fire rehabilitation (seed sowing, mulching) should be applied to ensure and/or facilitate the colonization of the burned sites by target species.

Chapter 3

Evaluation of grassland restoration techniques on former croplands in Europe

Summary

Grasslands were vital landscape elements throughout Europe. Nowadays, the area of grasslands is dramatically reduced, especially in the industrial countries. Their restoration is widely supported to increase the naturalness of the landscape and preserve biodiversity. We reviewed the frequently applied restoration techniques (spontaneous succession, sowing seed mixtures, transfer of plant material, topsoil removal and transfer) and techniques for improving species richness (planting, grazing and mowing) used to recover natural-like grasslands from ex-arable lands, focusing on their usefulness to restore biodiversity and their practical feasibility and costs. We conclude that the success of each reviewed technique depends on the site conditions, history, availability of propagules and/or donor sites, and on the budget and time available for restoration. Spontaneous succession can be an option for the restoration of grasslands in former arable lands when no rapid result is expected, and is likely to lead to the target in an area with high propagule availability. Sowing low diversity seed mixture is recommended when we aim at to create basic grassland vegetation in large areas and/or in a short time. The compilation of high-diversity seed mixtures for large sites is rather difficult and expensive; thus, it may be applied rather on smaller areas. We recommend combining the two kinds of seed sowing methods by sowing low-diversity mixtures in a large area and high-diversity mixtures in small blocks to create species-rich patches for spontaneous colonization. When proper local hay sources are available, the restoration with plant material transfer can be a fast and effective method for restoration.

Aims of the study

Despite the frequent application of grassland restoration in conservation practice, proportionally little attention has been given to its usefulness in biodiversity conservation. Recent reviews on grassland restoration have focused on species transfer, establishment and recovery which topics are highly relevant for both ecological theory and practice (e.g. Hedberg & Kotowski 2010; Kiehl et al.

2010). Arising from the great interest in grassland restoration by conservation practitioners, a review of the main methods of grassland restoration on former croplands, with a special emphasis on the applicability and cost-effectiveness of the methods is warranted.

Here we present a review of current practices in grassland restoration on former croplands. We first present the frequently used restoration techniques, and accessory techniques used to improve restoration success, with a listing of pros and cons of each method. Then, we evaluate restoration success based on the reviewed studies and finally, we summarise costs and make suggestions on the concrete application of the reviewed methods.

Our review was compiled using electronic sources (JSTOR, Science Direct, ISI Web of Knowledge and Google – keywords: “grassland restoration”, “grassland recovery”, also several recent articles were added based on the personal expertise of the authors. In our review we have included only those studies which were focused on grassland restoration techniques frequently used in croplands in Europe. For the cost issues we gathered information also directly from the authors of included papers.

Restoration techniques

Spontaneous succession

Spontaneous secondary succession following the abandonment of croplands, often termed as ‘old-field succession’, is the easiest and most natural way of grassland restoration (Prach & Hobbs 2008). Old-field succession is one of the best-studied topics in ecology and the knowledge gained in such studies (for a bibliography, see Rejmánek & van Katwyk 2005) has been instrumental in the development of the field of restoration ecology (Hobbs & Walker 2007). In some cases, restoration can rely on spontaneous processes (Ruprecht 2006; Prach & Řehouňková 2008; Török et al. 2010). In these cases, restoration is based on locally available sources of propagules, e.g. local seed bank or seed rain mediated by different seed dispersing agents from adjacent natural vegetation. In fragmented landscapes where the availability of adjacent seed sources is low and/or seed dispersing agents are missing, the regeneration of grasslands is often slow or delayed (Manchester et al. 1999; Simmering et al. 2006; Foster et al. 2007). Furthermore, agricultural cultivation in most cases completely destroys the former seed bank (e.g. the seed bank of grassland species) and results in an increase in the amount of seeds of weedy species in the soil (Bakker & Berendse 1999; Bossuyt & Honnay 2008; Manchester et al. 1999). The high amount of weed propagules associated with

higher levels of nutrients creates perfect conditions for weeds and their seedlings (Kardol et al. 2008), which hamper the regeneration process. Sometimes, succession stops in an early stage due to the increased dominance of a noxious competitor (Prach & Pyšek 2001). As a result, restoration by spontaneous succession in several cases can be slow or unpredictable. Thus, it is often necessary to direct vegetation changes with more active restoration measures.

Sowing seeds

Sowing seed mixtures of target species is a widely used restoration method in conservation practice (Table 2). The composition of a seed mixture is strongly influenced by the aim of restoration (e.g. target vegetation), the site conditions of receptor sites, or the availability of seed sources of potential target species. Low-diversity (LD) seed mixtures typically contain propagules of 2-8 species, which are usually the dominant grass and/or forb species of the target vegetation. High-diversity (HD) seed mixtures usually contain seeds of more than 10 species (Table 2).

The seeds for restoration can be purchased from commercial sources or collected by local harvesting. Commercial sources are appropriate if the seeds can be sourced from local populations of the target species. Seeds of rare species (characteristic grassland species usually in scattered populations, e.g. in loess grasslands - *Phlomis tuberosa*, *Thalictrum minus*; Török et al. 2010) are often not commercially available or very expensive, and often originate from non-native source populations (Manchester et al. 1999). Thus, the compilation of a HD mixture that also contains rare species can be unfeasible. It is advisable to use seeds collected or sourced locally or as close to the location of the restoration as possible (Mijnsbrugge et al. 2010). Sowing seeds from local sources decreases the chances of restoration failure due to the genetic incompatibility of the sown and naturally colonizing individuals of a species (Kiehl et al. 2010). Using local ecotypes also increases restoration success as such ecotypes are better adapted to the local environmental conditions and may be better competitors against local weeds (Aldrich 2002). Seeds can be collected by hand or by appropriate equipment (e.g. vacuum harvesting, combine harvester; Edwards et al. 2007). Though hand collection is time consuming and costly (Stevenson et al. 1995), it is important when target species are located in scattered populations.

When seeds of certain target species are not available in the same quantity as those of other, more common species, the sowing of LD and HD seed mixtures can be combined. The HD seed mixture can be sown in small patches within a larger area sown with LD seed mixture to establish potential sources of colonizing

propagules. Using LD seed mixtures can lead to the restoration of basic grassland vegetation dominated by perennial grasses as fast as in 3–4 years (Török et al. 2010). The immigration of rare herbaceous species can be very slow, so the restoration of diverse grasslands can last much longer than basic grassland vegetation. For the total recovery of species-rich vegetation further post-restoration management are often needed. Grassland restoration by seed sowing often but not always requires soil preparation or even topsoil removal to establish bare ground surfaces. Seeding on bare soil greatly enhances the establishment of the target species (Kiehl et al. 2010). Soil preparation is mostly done by deep or shallow ploughing or disking followed by seed bed preparation (by raking). Soil preparation is mostly done by deep or shallow ploughing or disking followed by seed bed preparation (by racking). After sowing the cover of seeds is necessary by light raking or ring rolling. The aim of topsoil removal is to significantly reduce the amount of weed seeds, and nutrient availability in the upper soil layers or to establish microsites favourable for germination of the target species (Coulson et al. 2001; Pywell et al. 2002; Edwards et al. 2007).

Grassland restorations vary greatly regarding the density at which seeds are sown. Many studies reported on seed sowing conducted in a few to a few hundred square meters. In these cases, sowing densities ranging from 4,000 to 13,000 seeds/m² were used. When grassland restoration is carried out in larger areas, sowing densities of 20–45 kg/ha were used (Table 2), some cases much higher densities are also suggested (80–500 kg/ha; if rapid recovery of grassy dominated swards is needed, see Krautzer & Wittman 2006). Increasing amounts of seeds often correspond with faster establishment of the target species (Lindborg 2006), but can also lead to higher rate of competition for resources among sown species. Stronger competitors (e.g. sown clonally spreading grasses) can become dominant on the cost of other sown target species. This can lead to decreasing target richness (Lepš et al. 2007).

Transfer of plant material

The transfer of fresh plant material, raked litter, or hay containing the seeds of target species is used in grassland restoration in two ways; either to start secondary succession after land abandonment, or to increase species richness of degraded grasslands (Rasran et al. 2006). Although the transfer of plant material (e.g. seed enriched barn chaff) was traditionally applied until the middle of the 20th century to improve hay meadows (Kiehl et al. 2010), here we focus only on transfers used to restore grasslands on abandoned fields. Under such conditions, the transfer of plant material is typical in restoration of species-rich grasslands, where the compilation of

a seed mixture, often containing over 50 target species, would be almost impossible (Table 3).

Important factors in the design of plant material transfers are the site conditions, the area of the receptor and the donor sites, and the timing of the collection of plant material. The ratio between the area of receptor and that of the donor site generally ranges from 1:2 to 1:10; depending on the species richness, propagule richness and quality of the vegetation in the donor site (Aldrich 2002; Edwards et al. 2007). The most appropriate time for collecting plant material is determined by the phenology of donor community and the target species, i.e. when the seeds of most species become ripe (Edwards et al. 2007). If we want to maximise the harvest of grass seeds the most appropriate mowing time is in dry grasslands (e.g. in alkali or sandy grasslands) in June, mesophilous grasslands between June and July, in wet grasslands usually in July to late August in Europe. However, the appropriate time of harvest is strongly dependent from actual weather conditions. Using plant material collected later, e.g. in late September, can lead to significant loss of propagules, especially that of graminoid species (Hölzel & Otte 2003). This can be a crucial problem in recovery of species poor and graminoid species dominated vegetation, like alkali grasslands (Török et al. 2010). As an alternative, seed collections may be repeated and spread across the vegetation period to maximise the number of target species (Stevenson et al. 1995). The collected plant material can be applied immediately, i.e. up to 24 hours after cutting (Pywell et al. 1995; Donath et al. 2007), or it can be dried and stored as hay (Edwards et al. 2007). The transfer of fresh plant material appears to result in a higher establishment rate of target species than that of dried material and may increase the chances of establishment of rare species (Kiehl et al. 2010), due to the loss of seeds during the drying or storing process. The fresh or dried plant material is usually spread at a thickness of 10-15 cm (Donath et al. 2007) or density of 1-2 kg/m² in the restored site (Kirmer & Mahn 2001; Kiehl et al. 2006). If the amount of propagules in the plant material is high, the quantity of hay can be reduced to 0.5-1 kg/m² (thickness of 3-5 cm) (Kirmer & Mahn 2001). The quantity of hay transferred is of central importance because if too much plant material is transferred per area, the thick plant layers can inhibit the germination and colonization of target species (Donath et al. 2006).

Topsoil removal and carbon addition

Some former croplands can be characterised by high nutrient loads arising from the use of chemical fertilizers on former croplands (Verhagen et al. 2001). High nutrient levels of the soil can favour weedy species after the cessation of the

agricultural cultivation (Eschen et al. 2007), which can slow down the restoration, and/or decrease its success (Patzelt et al. 2001; Hölzel & Otte 2003, Edwards et al. 2007). Two methods are most frequently used to decrease the amount of available soil nutrients in the upper soil layers: topsoil removal and carbon addition.

Topsoil removal can reduce the amount of available nutrients (Allison & Ausden 2004; Kardol et al. 2008). In addition, many of the weed propagules can be removed with the topsoil (Hölzel & Otte 2003). In most cases, the removal of the upper 25-50 cm of topsoil is enough to ensure favourable conditions for the restoration (Klimkowska et al. 2007). However large scale topsoil removal is not recommended in fields where high deflation by wind can be foreseen and also in steep slopes high exposed to soil erosion.

Another tool for decreasing soil fertility in the upper soil layer is the immobilization of nutrients, especially nitrogen, in the soil. Generally, the immobilization is executed by the addition of various carbon sources, which alters the C:N ratio in the soil (Török et al. 2000). The higher level of carbon in the soil often restricts microbial activity; therefore, it reduces the availability of mobile nitrogen for plant uptake (Averett et al. 2004; Eschen et al. 2007). Frequently used carbon sources are mulch (Averett et al. 2004) or hay (Kardol et al. 2008) and occasionally sucrose is used (Török et al. 2000; Eschen et al. 2007). However, the effect of nutrient immobilization by carbon addition is only a short-term solution compared to topsoil removal, because of the high microbial turn-over in the soil (Reever & Seastedt 1999).

Topsoil transfer, turf transplantation and community translocation

The success of restoration can be facilitated by the transfer of the upper soil layer from native grasslands. During a topsoil transfer, the upper layer of the soil is excavated, transferred to the restored site and spread in the form of mixed soil (Bullock 1998; Skrindo & Pedersen 2004). In the case of turf transplantation, smaller turfs are cut and transferred to the restoration site (Manchester et al. 1999; Aldrich 2002). Finally, community translocation means the transfer of an entire community; it is the rescue of a whole community from complete destruction (Bullock 1998).

One advantage of turf transplantation is that small patches of the target habitat can be created in the site subject for restoration. The transplanted turfs can serve as propagule sources for re-vegetation. The introduced vegetative plant parts and diaspores associated with the introduced soil fauna and micro biota make the re-vegetation quicker than would be occurring in the spontaneous way (Kirmer & Tischew 2006).

However, topsoil transport, either with or without vegetation, is not typically recommended as a restoration method, because it damages or destroys some parts of the donor site. In addition, the collection and the transfer of turfs and topsoil require considerable manpower and intense use of machinery, which can raise the costs to extremes (Table 4). The maximum distance of the transfer of turfs is often only several hundred of meters. The excavation of soil and turves is the simplest in loose and sandy soils, but the excavated material can easily fall apart during the transport. In heavy soils the excavation is much harder and only small turves can be transported because of high specific weight of the soil. In most cases high specific survival rates were reported (54-90% of species were successfully survived the transfer; Bullock 1998) but in some cases high mortality of the transferred plants was reported. For example, only 16% of the grassland species survived in a translocation project in NW Hungary; where 4×1×0.6-m blocks of topsoil were transferred (Takács G., pers. comm.).

Accessory techniques used to improve restoration success

These techniques are widely used to increase the availability of seeds of target species either by planting entire plant individuals or introduce seeds, and help plant establishment by grazing animals or by mowing.

Planting

Species richness in the restored grasslands can be improved with the plantation of entire plant individuals, or belowground parts (e.g. rhizomes, bulbs) of plant individuals. In addition, the selective planting of late-successional species in early successional stages can greatly accelerate restoration success (Du et al. 2007). The planting of belowground parts are used for species with good vegetative reproduction and establishment capabilities (Kirmer & Tischew 2006). Planting, however, is a cost-intensive method. It is recommended only in cases when the immediate translocation of endangered plant populations is necessary. This technique is often used to improve species richness or the availability of propagules in seed sowing or hay-transfer restored fields.

Grazing and mowing

Once basic grassland vegetation was established, mowing and/or grazing can be used to facilitate the colonisation of further characteristic species and increase plant diversity. Grazing and mowing generally accelerate the restoration, but they

can also create conditions under which the restoration process is hampered. Both grazing and mowing have an extensive published literature (e.g. Bakker 1989); here we focus only those studies in which some practical aspects for post-restoration are discussed. The most important effect of grazing and mowing is the reduction of the aboveground biomass (Diemer et al. 2001; Bonanomi et al. 2006; Billeter et al. 2007). A common phenomenon in grassland restorations in former croplands is that an intensive plant biomass and litter accumulation is observed from the first year onwards (e.g. biomass and litter of sown grasses). The accumulated litter can often several times exceed the amounts typical for target grasslands (e.g. Török et al. 2010) and can hamper the establishment and immigration of further target species. The removal of accumulated litter by grazing and mowing can be highly beneficial to post-restoration processes as litter removal can open up niches for further colonisation of target herbs from adjacent vegetation, if available (Bissels et al. 2006). However, gaps provide also physical space for the germination and establishment of weedy species present in the seed bank, especially in that of former croplands. An evaluation of the seed bank is essential to ensure that ecological processes progress towards the target status and not towards a weed-dominated phase (Török et al. 2009). Gaps originated from grazing can also favour the immigration of non-grazed noxious and poisonous invaders (e.g. *Asclepias syriaca* in degraded sandy grasslands; Csontos et al. 2009).

Grazing has several advantages for grassland restoration compared to mowing. First, grazing can be more efficient in introducing propagules of the target species. Grazing animals bring in propagules of the target species from target-state grasslands through their guts or on their fur in the receptor sites (Fischer et al. 1996; Mouissie et al. 2005; Mann & Tischew 2010). Mowing is less likely to have such an advantageous effect, although it is possible that propagules attached to the mowing machinery can be introduced into the receptor sites (Bakker et al. 1996). Second, grazing pressure is more likely to vary in space, especially when grazing is conducted by horses, which may create a more mosaic-like habitat structure. In contrast, mowing by heavy machinery often leads to homogenization of the plant community locally and at the landscape level (Zechmeister et al. 2003). In addition, mowing by large machinery also increases the compactness of the soil (Schäffer et al. 2007), which can also reduce the success of colonization of target species. When mowing is done by hand, it can mimic an uneven distribution of disturbance necessary to create species-rich grasslands (Bissels et al. 2006). However, post-restoration management by hand mowing is costly or unfeasible in larger areas.

Livestock grazing is highly selective, which could negatively affect the target species. For example, most of grazing animals (e.g. cattle and sheep) usually avoid thorny or woody plants, which may lead to an increase of such plants and decrease

the abundance of target native species (Hayes & Holl 2003). Furthermore, trampling and overgrazing of livestock over grasslands enhance species that well tolerate such disturbances, but detrimental to species that are sensitive to trampling (Belsky & Blumenthal 1997). The intensity of grazing and the frequency and timing of mowing are crucial in influencing the success of restoration (Dostálek & Frantík 2008).

For grazing, the identity of livestock is also important. Cattle provide a rather even distribution of grazing pressure; however, their selective grazing benefits the establishment of thorny or woody herbs and trees (Hayes & Holl 2003). To avoid the invasion of thorny and woody species goat grazing is a useful solution (Celaya et al. 2010). Grazing by sheep can result in a homogeneously low vegetation height, but may also damage plants of conservation importance, especially in wetter habitat types.

Mowing is generally more cost-effective and more readily available as a management option than grazing, which needs to encompass infrastructural and manpower investments (fencing, electric fencing, shepherds) over longer periods. However, mowing can result in high direct mortality and lower densities of invertebrates, whereas grazing is less directly damaging to invertebrates and can provide additional niches for invertebrates, e.g. to decomposers of animal droppings (Humbert et al. 2009). In general, a more complex food-web is expected in grazed areas than in mowed areas (Wang et al. 2006).

Restoration success

The overall success of each restoration technique discussed above is difficult to assess for several reasons. First, each restoration technique may be suitable for certain starting conditions and target states and a comparison of very different techniques can be misleading. Second, even when similar techniques are used, there is high variation in the technical details of how restoration was carried out (Table 2). Finally, the measure of restoration success reported often varies among the studies, which makes a direct comparison difficult. Evaluation of the success of each technique to restore target grasslands is meaningful only for those techniques which are similar enough with regard to starting conditions, main methods and measure of success. Restorations based on seed sowing and transfer of plant material offer a possibility for such a comparison. Furthermore, spontaneous succession, particularly when monitored along with seed sowing or hay transfer in the same study, offers a useful reference against which to judge the success of the more active restoration technique.

Restoration success after seed sowing and spontaneous succession

Data for a comparison of relative restoration success were available from nine studies reporting the effects of sowing HD seed mixtures, seven studies on LD mixtures and seven studies on spontaneous succession (Table 2). Especially valuable are those studies that monitored several treatments (seed mix diversity, spontaneous succession) simultaneously, under the same settings (Table 2).

A detailed analysis of establishment success (Table 2) suggests that sowing HD seed mixtures lead to faster establishment of the species targeted by the restoration than an LD mixture or spontaneous succession. The richness of established species increased with the number of sown species in most restorations and in the two experiments directly testing the effect of sown species richness on establishment success (Manchester et al. 1999; Piper et al. 2007). However, in some cases, even sowing HD seed mixtures cannot guarantee fast establishment success. For example, both Stevenson et al. (1995) and Lawson et al. (2004) reported very poor establishment of the sown species. The establishment of sown species is often delayed until after Year 1 following restoration (Vécrin et al. 2002). In other cases, establishment was highly successful even in Year 1 (Manchester et al. 1999). Even though sowing HD mixture increases established species richness compared to sowing LD mixture or spontaneous succession, sowing HD seed mix may also constrain the colonisation of late-succession species (Lepš et al. 2007). In the study of Lepš et al. (2001) they found that in the first few years after restoration, usually LD seed mixtures led to less diverse communities than HD ones. They also found that the best LD seed mixture can approach the species richness obtained by HD seed mixture (Lepš et al. 2001). Lepš et al. (2007) studied the same sites for longer time-scales (6-7 years) and found that species richness in HD sowing decreased below that in LD sowing. They detected slightly fewer established species in HD restorations compared to LD restorations in each of the five European countries studied (Table 2). However, over longer time scales, more unsown species colonized LD restorations than HD restorations (Lepš et al. 2007; Table 2).

Other observations also confirm these contrasting patterns. For example, species richness often decreases in sown plots and increases in naturally re-vegetating plots with time, sometimes even surpassing species richness in the sown plots (Jongepierová et al. 2007). These observations suggest that the sown grass community reduces the possibility of further colonization by late-successional species by competitive exclusion or litter accumulation (Lepš et al. 2007; Török et al. 2010). Therefore, the initial floristic composition hypothesis (Egler 1954), which predicts that early processes largely determine the outcome of restoration, may

explain short-term changes following grassland restorations, but is not supported by longer-term experiments (Table 2).

We identified three shortcomings of grassland restoration experiments carried out with seed sowing. First, generally little attention is paid to some starting conditions (e.g. seed content of the soil) and site history. For example, previous crop type on the abandoned arable land is only rarely given in the studies reviewed here, even though crop type and the corresponding cultivation (use of fertilizers, pesticides etc.) can greatly determine restoration success. For instance, some crop types require more fertilizers/pesticides than others, which may influence both the amount of nutrients available for restoration and the insects that may provide important ecological services such as pollination (Stoate et al. 2001). Moreover, some crops can produce allelopathic chemicals, which could hamper the establishment of target species especially in the early years (e.g. sunflower, Leather 1987). Site history is neglected even in studies focusing exclusively only on spontaneous processes (but see Molnár & Botta-Dukát 1998).

The second problem is that high concentrations of soil phosphorous or other nutrients on abandoned cropland can limit the success of colonization by several target species due to the increased competition from a few dominant grasses caused by high nutrient availability (Gough & Marrs 1990). The majority of the studies reviewed here did not typically report initial nutrient loads and did not consider this effect during the design of restorations (but see Van der Putten et al. 2000; Lepš et al. 2001; Pywell et al. 2002). As a remedy, Marrs (1985) suggested topsoil removal, deep ploughing or some post-restoration management to reduce high nutrient loads or the high cover of the few dominants. The decrease of the amount of available soil nutrients is also possible by regular biomass harvest. However, Marrs et al. (1998) showed that the amount of available nutrients was not significantly changed in a seven year study of cropping. Which suggest that this method of nutrient decreasing may effective only in the long run (more than 10 years).

Restoration success after plant material transfer

Data for a comparison of relative restoration success following plant material transfer in former croplands were available from six studies (Table 3). The success of plant material transfer depends on the availability of high-quality donor sites. If suitable initial conditions are met (e.g. high-quality of plant material, low nutrient availability), the application of plant material transfer provides rapid establishment of the target species (Patzelt et al. 2001; Kiehl et al. 2006; Donath et al. 2007). Concrete measures of establishment success are available only when the seed content of plant material and the species composition of donor site are studied

(Hölzel & Otte 2003; Kiehl et al. 2006; Rasran et al. 2006; Donath et al. 2007). The transfer rate of species depends strongly on vegetation type and site conditions of the donor site. The transfer rate of species varies between 20% and 80%. The number of transferred species can be enhanced by the combination of early and late-harvested plant materials (Kiehl et al. 2006). An advantage of this method is that the transferred plant material may effectively suppress weeds. Conversely, the germination of the transferred species was not hampered or was facilitated by plant material cover (Kirmer & Mahn 2001; Hölzel & Otte 2003; Donath et al. 2007). In one of the most comprehensive long-term study of plant material transfer, Kirmer & Mahn (2001) found that the number of established target species rapidly increased during the first five years; later on this process slowed down, even some of the transferred poor competitor species disappeared, caused by the increased dominance of a strong competitor (Kiehl et al. 2006).

We found several general shortcomings which can constrain the use of plant material in restoration. First, the seed content and species composition of hay is difficult to determine. In most cases, only the species composition of the used plant material and/or the vegetation of the donor site is determined. The propagulum-content of the transferred plant material is rarely studied (but see Hölzel & Otte 2003; Rasran et al. 2006; Donath et al. 2007). Second, the vegetative propagules (e.g. tillers and rhizomes) of asexually reproducing species (e.g. several *Carex* species; Hölzel & Otte 2003) cannot be transferred in the form of cut plant material, therefore, the direct seeding or transplanting of individuals of these species is necessary (Pywell et al. 1995). Third, the use of this method requires donor sites of appropriate size and quality. This constraint strongly limits the area that can be restored. Two- to ten-times higher area of donor sites are required than that of the receptor site to effectively transfer target species with plant material (Aldrich 2002; Kirmer & Tischew 2006; Edwards et al. 2007). The use of low-quality plant material (e.g. originating from species-poor or weedy grasslands) can direct vegetation changes to unsuitable directions, and can result in a weed domination (Hölzel & Otte 2003; Donath et al. 2007). So, the upper limit of the area that can be restored by this method is often a few hectares, especially where only small fragments of suitable donor sites are available.

Costs of restoration

In restoration planning is crucial to know costs of restoration actions. Most of the studies included in this review were no cost estimates provided (but see Manchester et al. 1999). Based on our own expertise and kindly help of several authors we summarised reporting direct costs of various restoration actions from

several European countries in this review (Table 4). We considered direct costs the followings: (i) plant material/seed (if any), (ii) seed collection/plant material harvest/soil collection/soil removal (if any), (iii) storage and transfer costs (if any), (iv) site preparation (ploughing, disking, seed bed preparation, if any), (v) sowing, spreading costs (if any), (vi) some additional management costs (if any, e.g. mowing, mulching or several additional techniques used in the first year of restoration).

The cheapest method is readily the spontaneous succession where only some costs of regular mowing or grazing can be foreseen in the restoration sites (to improve immigration of target species and decrease cover of weeds). The cheapest active restoration measure is the sowing of low diversity seed mixtures. Based on our query a several hundred euro per hectare costs can be expected (185-548 €/ha). Using a high diversity seed mixture at least two-times higher costs can be foreseen (typical scores were around 1000 €/ha). The cost is highly dependent from the sowing density and species richness of the used mixture. The cost for plant material transfer ranged from several hundred €/ha in (Hungary and Poland) to several thousand €/ha (Germany). Costs were strongly dependent from the (i) country it was used, (ii) the grassland type, (iii) size of donor area (small patches is more difficult and costly to harvest e.g. by hand) and the (iv) thickness of transferred plant material applied in the receptor site. Topsoil removal and community transfer actions are even more costly. The costs of topsoil removal can exceed 10,000 €/ha (Marrs et al. 1998; Klimkowska et al. 2010b). In case of community translocation the costs can be astronomical if we try to transfer also the deeper soil layers of the transferred community (Table 4). During the planning of grassland restoration it should be taken into account that there are several national and/or EU subsidies and projects which can cover entirely or partly the cost of grassland restoration actions.

Implications for practitioners

There is a need for well documented and planned case studies of direct restoration actions worldwide so we encourage practitioners and site managers planning a grassland restoration in former croplands to follow the forthcoming suggestions:

- Restoration measures should be chosen according to specific site conditions: the area, soil type and former use of the cropland subjected to grassland restoration. Consultation with local experts is recommended to identify the target vegetation (in terms of structure, species composition and management) of restoration.

- Consult with experts in your country for help to choose the proper restoration method in accordance with your financial background, manpower and other investments needed.
- Before a restoration action it is worth to look for subsidies in your country to cover at least partly the restoration costs. Plan also the post-restoration management which is proper for the selected target grassland type (e.g. mowing or grazing). Make sure that post-restoration management is sustainable in the long run at your restoration site and also calculate the future costs for the management measures.
- Document the restoration process in detail as a reference for further actions (e.g. the composition and density of seed mixture, origin of the mixture, sowing procedure).
- Select suitable indicators for measuring restoration success.
- Long-term monitoring, evaluation and publication of the results after restoration is very important to identify 'best practices' and potential drawbacks.

Chapter 4

Weed suppression after grassland restoration by seed sowing – the role of litter accumulation and seed banks

Summary

Grassland restoration on former croplands offers good opportunity to mitigate the loss of grassland biodiversity. Weed suppression can be another benefit, which becomes increasingly important because of the high recent rate of abandonment of arable lands in Central and Eastern Europe. Our aim was to evaluate the usefulness of sowing two low-diversity seed mixtures followed by annual mowing, a frequently used restoration technique, in weed suppression. We found that rapidly forming cover of sown grasses effectively suppressed short-lived weeds and their germination except in the first year. We found significantly lower forb biomass in the second and third year, than in the first year after sowing. Litter and biomass of graminoids increased significantly during the study, and correlated negatively with the biomass and species richness of forbs. Our results suggest that accumulation of litter and graminoid biomass is beneficial in suppression of weedy forbs, but may also hamper the immigration of target species. The detected dense seed bank of short-lived weeds points out the possibility and threat of later weed infestation. In the short run perennial weeds cannot be suppressed easily by sowing and annual mowing. We found that the effectiveness of seed sowing followed by mowing in weed suppression can be different on sites with different history or seed mixture. Rapidly establishing perennial weeds, such as *Agropyron* species were only detected in former alfalfa fields; *Cirsium arvense* was found in former cereal and sunflower fields but not in former alfalfa fields. We found that the rate of weed suppression and success was influenced by the seed mixtures used. In several alkali restorations the high proportion of perennial weeds was detected in year 3. In loess restorations, much lower scores were typical. This was likely caused by the different seed mixture used. The loess seed mixture contained seeds of a clonally spreading tall-grass, *Bromus inermis*, which could compete more effectively with clonally spreading weeds, than could short grass species with or without tussock-forming.

Aims of the study

We studied the effects of litter and biomass of sown grasses on species richness and biomass of early colonising forbs in former alfalfa fields sown with low-diversity seed mixtures in Hortobágy National Park. 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, while changes in biomass are typically neglected.

We measured biomass of litter, forbs and sown grasses. We also studied the short-term vegetation dynamics and soil seed banks of restored grasslands on former croplands in the first three years after seed sowing. We asked the following questions: (i) What is the effect of the accumulating biomass of graminoids and litter on the biomass of early colonisers? (ii) Is the amount of graminoid biomass 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 native grasslands? (iv) Which weed species groups are likely to be suppressed by this way of restoration? (v) Can the success of weed suppression be compromised by the re-establishment of weed vegetation from soil seed banks?

Materials and Methods

Sampling setup

We studied ten former alfalfa fields sown with low diversity alkali (4 fields) and loess (6 fields) seed mixtures. Grassland restoration was carried out as part of a LIFE-Nature project (<http://life2004.hnp.hu/index.html>) in the 'Egyek-Pusztakócsi mocsarak' marsh and grassland complex in Hortobágy National Park (East Hungary, N 47° 34' E 20° 55'). The elevation of the area is between 87 and 98 m a.s.l. The climate is moderately continental, characterised by a mean annual temperature of 9.5 °C and a mean annual precipitation of 550 mm. The soil of the studied fields were moderately compact (loam or clay-loam), with a pH (H₂O) of 6.0-7.6, and was characterised by low salt (< 0.02%) and CaCO₃ (< 2%) contents. In all fields high phosphorous (typically 500-700 mg/kg) and potassium (typically 400-600 mg/kg) contents were measured, which frequently occurs after long-term crop production.

Seed mixtures were sown in a density of 25 kg/ha following soil preparation in October, 2005. Alkali seed mixture contained the seeds of *Festuca pseudovina* and *Poa angustifolia*; while loess seed mixture contained the seeds of *Festuca*

rupicola, *Poa angustifolia* and *Bromus inermis*. The fields were mown once in June every year after sowing.

For the study one 5×5 m sized sampling site per field was randomly marked. In each site 10 aboveground biomass samples (20×20 cm sized) were collected in June before mowing, in every year between 2006 and 2008. The species list of forbs in every biomass sample was recorded. Samples were dried (65°C, 24 hours), then sorted as litter, graminoid (*Poaceae* and *Cyperaceae*) and forb (non graminoid monocots and dicots). The forb biomass collected in the sown fields was sorted to weed and non-weed species groups according to Grime's CSR strategy types (Grime 1979) modified and adapted to Hungarian conditions by Borhidi (1995). The dry weights of the biomass samples were measured with 0.01 g accuracy.

In every sampling site, four 1×1 m plots were permanently marked. In the plots, the cover of vascular plant species was recorded in early June before mowing in the first three years after the sowing.

Seed banks of sown grasslands were sampled in the third year after sowing when the perennial cover was closed. Samples were collected after natural winter stratification and snowmelt in the plots for vegetation recording, in late March of 2008. We bored three soil cores per plot (4 cm in diameter, 10 cm in depth, 126 cm³/core, and altogether 12 cores per sampling site); 120 soil cores in total. Cores from the same plot were pooled to reduce sample heterogeneity. Sample volume was reduced by 60-80% by the sample concentration method of ter Heerdt et al. (1996). Vegetative organs were separated by washing over a coarse sieve (3 mm mesh size), while seed-free fine soil components were removed using a 0.2 mm-fine mesh. Concentrated samples were spread in a thin layer (maximum thickness about 3-4 mm) on trays, previously filled with steam-sterilized potting soil. Trays were placed under natural light in a greenhouse shaded from early May to August. Seedlings were regularly counted, identified then removed. Unidentified plant specimens were transplanted and grown until they could be identified. In early July, when no seedlings emerged, regular watering was stopped, and the dried sample layers were crumbled and turned. In early September, watering was re-started and continued until early November. Occasional seed contamination (e.g. dispersal by wind) was monitored in sample-free control trays filled with steam-sterilized potting soil.

For reference (restoration target) alkali (*Achilleo setaceae* - *Festucetum-pseudovinae*) and loess (*Salvio nemorosae-Festucetum rupicolae* with *Bromus inermis* dominance) grasslands were also sampled in 2008 using the sampling design for vegetation and biomass recording as described above.

Data processing

The temporal dynamics of biomass in the sown fields (e.g. mean scores of litter and graminoid biomass) was compared with repeated-measures ANOVA and Tukey test (Zar 1999) on field levels, averaging the samples from the same field ($N=4$ for alkali and $N=6$ for loess seed mixture sown fields). The differences of biomass 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). We calculated the heterogeneity of graminoid biomass and litter using the Gini-coefficient (Zar 1999). Correlation between litter, graminoid biomass and the biomass 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).

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

Weed species were selected based on Grime's ruderal species group (1979), as adapted to local conditions in the Social Behaviour Types general classification of Borhidi (1995) and fine tuned by the personal expertise of the authors in alkali and loess vegetation. The species groups AC (adventive competitors, e.g. *Conyza canadensis*, *Ambrosia artemisiifolia*), RC (ruderal competitors, e.g. *Cirsium arvense*, *Agropyron repens*) and W (mostly annual and biannual weedy grasses and forbs of low competitiveness) were considered as weeds. We classified all detected species into functional groups based on simplified life-form categories (*short-lived*: Th, TH and *perennial*: H, G, Ch) and morphological features (*graminoids* = Juncaceae, Cyperaceae and Poaceae, and *forbs*). Nomenclature follows Simon (2000) for taxa and Borhidi (2003) for syntaxa.

Results

Temporal changes of biomass in sown fields

Total biomass 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/m² to 696-789 g/m², 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 biomass 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 biomass 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 1). Total graminoid biomass 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 1).

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. 2). No significant changes were found in litter scores between Year 2 and Year 3, regardless of the seed mixture sown. Forb biomass 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 biomass (including 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 $N=6$, $F=52.93$, $p<0.001$). Biomass scores of forbs remained low (less than 18 g/m² in every sown field) from Year 2 onwards. Coinciding with the decrease of forb biomass, 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: $N=6$, $F=38.50$, $p<0.001$). Forb biomass and species richness showed a medium strong negative correlation with graminoid biomass and a strong negative correlation with litter (Table 5).

Biomass dynamics in sown fields and native grasslands

In Year 3, we observed significantly higher graminoid biomass in alkali restorations compared to native alkali grasslands (one-way ANOVA, $N=10$, $F=27.40$, $p<0.001$). The mean scores of graminoid biomass detected in the alkali restorations ranged from 616 to 1112 g/m², whereas these scores were much lower in native grasslands (range 140 - 178 g/m²). In loess restorations, graminoid biomass scores (range 468 - 987 g/m²) were not significantly higher than that of the native loess grasslands (range 262 - 520 g/m²), although high scores were more common in loess restorations.

In Year 3, significantly higher litter scores were found in alkali restorations than in native 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 native alkali grasslands (ranges 175 - 353 in restorations and 51 - 72 g/m² in native grasslands). Similarly to the graminoid biomass scores, no significant differences were found in the litter scores between loess restorations and native loess grasslands, although scores were slightly higher in the sown fields (range 130 - 466 g/m² in restorations and 95 - 273g/m² in native grasslands).

The heterogeneity of litter and graminoid biomass was highest in Year 1, and much lower scores were typical in both restorations in later years (Fig. 1 and 2). No significant differences were found between the heterogeneity of litter and graminoid biomass in Year 3 in restorations and in native grasslands.

Vegetation changes

The mean total species richness and the species richness of short-lived weeds were the highest in the first year and thereafter a tendency of decrease was typical both in alkali (Table 6, RM ANOVA, $P < 0.001$) and loess restorations (RM ANOVA, $P < 0.001$). A high cover of short-lived weeds was detected in almost every field in the first year (for detailed changes see Table 7). After the first year, a sharp decline in the cover of short-lived weeds was typical, in parallel with an increase of sown grass cover, which was detected in every field (RM ANOVA, for alkali restorations $P < 0.001$; and for loess restorations $P < 0.001$; Table 7). By the third year, perennial species became dominant (mostly perennial sown grasses) in every field (Table 7).

In several fields a considerable cover of a few species of perennial weeds was detected which were not found in considerable cover in native target grasslands (Table 8). In most alkali restorations, a high or increasing cover of perennial weedy *Agropyron* species was typical (Table 7). In two fields sown by alkali seed mixture (A1 and A2) the cover of *Agropyron* species increased during the three years (RM ANOVA, $N = 4$, the detected increase was significant for A1: $P < 0.001$, $F = 25.83$). Conversely, in most loess restorations either a low cover (typically lower than 5%) or a decreasing cover of perennial weeds was detected after the first year.

Seed bank and vegetation

The mean total seed bank density ranged from 9,417 to 22,215 seeds/m². Most scores were typically within the range of 11,000 and 18,000 seeds/m². Out of the 20 most frequent species of the seed bank, there were 12 weed species representing almost 70% of total seed banks and 70% of total seed bank density. We found considerably dense seed banks of short-lived weed species in all fields regardless of

the sown seed mixture (Table 9). The most frequent seed bank species, *Capsella bursa-pastoris*, was detected in almost all fields with high density. For most of the weed species no such clear trends were found. Only a few non-weedy forbs had a considerable dense seed bank. *Gypsophila muralis* and *Matricaria chamomilla*, characteristic short-lived pioneers of alkali grasslands showed high density only in alkali restorations. Seeds of wind-dispersed and small seeded hygrophytes (such as *Typha* sp. and *Epilobium tetragonum*) were found in every sown field. The sown grasses had mostly sporadic seed banks, only *Poa angustifolia* had considerably dense seed banks (up to 1,260 seeds/m²). We found mostly low-density seed banks of perennial weedy forbs (typically up to a few hundred seeds/m²), and no seed banks were found for perennial weedy graminoids (Table 9).

Species composition of the seed bank showed the highest similarity with the species composition of the vegetation of the first year (Jaccard similarity ranged from 0.16 to 0.38). The mean scores of similarity significantly decreased from Year 1 to Year 3 in both types of seed mixtures (RM ANOVA, $P < 0.001$). Several short-lived weed species that were detected with a high cover in first-year vegetation and suppressed later had a considerably dense seed bank (e.g. *Capsella bursa-pastoris*, *Matricaria indora*). Some other short-lived weeds such as *Fumaria officinalis*, *Fallopia convolvulus*, *Bromus arvensis*, *Papaver rhoeas* and *Veronica hederifolia* possessed only very sporadic seed banks. Conversely, several short-lived weed species detected with very low cover had considerably dense seed banks (*Setaria glauca* and *S. viridis*).

Discussion

Changes in biomass and litter

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

In our study, the highest total biomass scores were detected in the first year, conversely to Lepš et al. (2007), where an increase of biomass was detected after sowing from the first year to the second. In Lepš et al.'s (2007) study, the mean total biomass scores were at 300 g/m² in the first year; these scores increased in the second year to 430-720 g/m² 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/m²). 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 biomass.

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; Lepš et al. 2007; Foster et al. 2007). Our results confirmed that this increase of sown species holds also for the increase of their biomass. We detected a rapid accumulation of graminoid biomass 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 biomass increase also supports the theory that the speed and success of grassland recovery is 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/m² to 280-290 g/m² 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/m² 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 biomass production of sown grasses, but further, long-term monitoring of changes after restoration is necessary to explore sophisticated details of the processes in biomass changes (Virágh et al. 2008). We found a strong negative correlation between litter and forbs (both biomass 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 200 g/m².

Grassland recovery and weed suppression

We found contrasting short-term success of weed suppression in our study in relation to specific life history traits. Short-lived weeds (both forbs and graminoids) were effectively suppressed by sowing low-diversity seed mixtures and mowing as a post-restoration management in every sown field. The cover scores of short-lived weed species were reduced from a mean of 64-67% in Year 1 to a mean around 2% in Year 3. Similar results were detected in other grassland restoration studies using low or high-diversity seed mixtures (Lawson et al. 2004; Critchley et al. 2006;

Jongepierová et al. 2007; Lepš et al. 2007). Short-lived weeds are easily suppressed because of their (i) poor competitive ability (Tilman 1982), (ii) missing persistent seed banks, as was found for several species in this study, (iii) germination failure by a physical barrier or shading by both accumulated litter and green biomass (van der Putten et al. 2000), and also germination inhibition by discharged allelochemicals (Ruprecht et al. 2008).

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

The proportion of the above mentioned perennial weeds increased mainly in alkali restorations, while in loess restorations, much lower scores were typical. This was likely caused by the different seed mixture used. The loess seed mixture contained seeds of a clonally spreading tall-grass, *Bromus inermis*, which could probably compete more effectively with clonally spreading *Agropyron* spp. than could short grass species with or without tussock-forming like *Poa angustifolia* or *Festuca pseudovina* (e.g. Pywell et al. 2003).

These perennials have an effective clonal reproduction and vegetative spreading strategy by lateral tillers, so they can survive soil preparation and sowing practices and can rapidly establish through vegetative spreading by tillers (Lepš et al. 2007; Prach et al. 2007). This was also suggested by Pywell et al. (2003), where the performance of a species in restoration in former croplands were significantly favoured if the species was capable to effective vegetative growth and spreading. The rapidly increased cover of perennials detected in our study can be also supported by high nutrient levels in the soil, which is a result of previous use of fertilisers common in crop production. To suppress these perennial weeds, more intensive management practices are necessary. Increased mowing frequency (for *Agropyron repens*; Parr & Way 1988) can be a proper solution for decreasing the cover of the perennial weeds detected.

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

Seed banks

We found that several short-lived weeds that were effectively suppressed (e.g. *Capsella bursa-pastoris*, *Matricaria inodora*) or not even detected in aboveground vegetation (e.g. *Setaria viridis*, *S. glauca*) had considerably dense seed banks, which offers a possibility for their later establishment. This result clearly indicates that weed suppression aboveground means not necessarily the elimination of even the short-lived weeds from restoration sites.

The seed density scores for weeds detected in our former fields fit in the lower part of the previously detected range of seed density scores for weeds in agricultural lands (250 - 130,300 seeds/m²; Cavers & Benoit 1989). Several short-lived weeds detected in this study with sporadic seed banks can be completely eliminated from restoration fields (e.g. *Fumaria officinalis*, *Bromus arvensis*). For several short-lived weed species, very long-term persistence, reaching up to several decades, was proven (Thompson et al. 1997; Davies et al. 2005). Regular cultivation by creating bare soil surfaces can cause a rapid germination of several weed species and also decrease the density of their soil seed banks (Lutman et al. 2001). The rapidly formed cover of perennials in our study suppressed short-lived weeds aboveground and prevented the germination of weeds (except in the first year), but may have allowed the preservation of their seed banks. The re-establishment of weeds from this seed bank can be enhanced by creating gaps in the vegetation; thus, management actions that increase suitable vegetation gaps, such as grazing/trampling by cattle or sheep, and also other types of soil disturbance should be avoided in the first years after restoration (Renne & Tracy 2007).

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 native grasslands. This was only partly supported by our findings. Much higher litter and graminoid biomass was detected in restored fields than in native grasslands, but the evenness of both scores was similar in restored and native grasslands. The detected scores of

litter and graminoid biomass in Year 3 were higher than scores in native grasslands. Both litter (130-466 g/m² in Year 3) and graminoid biomass scores (701-905 g/m² in Year 3) were higher than scores detected during grassland recovery in extensively managed alfalfa fields in the study region (up to 165 g/m² litter and up to 253 g/m² graminoid biomass in 1- to 10-year-old fields; Török et al. 2010). The higher biomass and litter production detected in the present study was probably supported by the residual surplus of soil nutrients typical after the termination of agricultural cultivation, found also in other studies of grassland restoration (Pywell et al. 2002; Foster et al. 2007; Török et al. 2010). Increased biomass 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, litter and graminoid biomass accumulation can also hamper the establishment of several characteristic grassland species by (i) competitive exclusion (Foster & Tilman 2000) and/or by (ii) decreasing gap availability (Facelli & Pickett 1991; Anderson 2007; Ruprecht et al. 2010).

General conclusions

The dissertation stressed the management and restoration perspectives of European grasslands with a special focus on alkali grasslands. In the first chapter of the dissertation we introduced alkali grassland types and we reviewed their management, conservation problems and restoration perspectives. In the second chapter we evaluated the potential use of prescribed burning as a substitutive management and restoration tool in European grasslands. In the third chapter, we provided a review of the frequently used restoration techniques, focusing on their usefulness to restore biodiversity and their practical feasibility and costs. In the final chapter, we studied grassland restoration by seed sowing as a potential tool in weed control.

We found that carefully designed prescribed burning offers a vital solution and an appropriate and cost-effective substitution to grazing and mowing. Prescribed burning is an integral part of the North-American grassland conservation practice, while in European grasslands it is rarely applied. European studies on this topic are scarce, and mostly yearly dormant-season burning is used. The reviewed studies concluded that yearly burning solely is not an appropriate option to preserve and maintain species-rich grasslands. We discussed burning studies from North-America to identify which findings can be adapted to the European grassland conservation strategy. In North-America, contrary to Europe, the application of burning is fine tuned in terms of frequency and timing, and generally combined with other restoration measures (grazing, seed sowing or herbicide application). Thus, multiple conservation goals, like invasion control and increasing landscape-level heterogeneity can be linked. We found that one of the major constraints in the application of burning in European grasslands is the lack of related case studies. We emphasize to include planning evidence-based conservation issues regarding the application circumstances of burning (e. g. timing, frequency) and grassland types where it can be an appropriate management tool. There is a lack of knowledge about the effects of burning on certain rare and endangered species so the application of burning on areas with remnant populations is not recommended. First, experimental approaches should be tested, e.g. burning smaller patches within a grassland site, preferably of a lower conservation value. Burning larger grassland areas or sites with high conservation value requires experiences and conclusions drawn from experimental, small scale burning studies.

We found that the applicability and success of each grassland restoration technique depends on (i) the present site conditions, (ii) site history, (iii) availability of donor sites and propagule sources, and (iv) on the budget and time available for

restoration actions. We suggest that further, carefully designed studies are needed to make a more precise evaluation of the applicability of each technique. First, different restoration techniques should be applied in similar site conditions and circumstances to compare their relative success. Second, the applicability of each technique should be tested in restoration of several grassland types with the same study design. Finally, it is advisable for further studies to report most carefully detailed information about the implementation of restoration actions and make conclusions about the restoration success.

We pointed out that spontaneous succession can be an option during the restoration of grasslands in former arable lands. This kind of restoration usually does not demand different kind of interventions. The recovery of grassland vegetation in spontaneous succession compared to technical restoration is often slower and often un-directional. Applying this method 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 use of a low-diversity seed mixture is recommended when the aim is 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. As the compilation of the proper amount of high-diversity seed mixture for a large area is rather difficult, high-diversity mixture may be applied rather on comparatively smaller sites. In the application of both types of mixtures it is necessary to use seeds of regional provenance to avoid establishment failure by not appropriate ecotype or genetic incompatibility. Based on the reviewed studies a sowing density up to a maximum of 40 kg/ha is recommended to avoid extremely high competition and this density is reasonable if cost-effectiveness is taken in account. To enhance biodiversity, we can combine the two kinds of seed sowing methods: in a large area, we sow low-diversity mixtures (e.g. in a density of 20-25 kg/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 40 kg/ha) to establish species rich sites. From these created species rich patches further species can disperse into the low diversity mixtures sown parts facilitated by mowing or grazing. It is important that in use of seed mixtures seeds of regional provenance must be used. The use of plant material transfer is recommended in the restoration of smaller areas. Its usage depends on the available plant material sources. If there are no local sources, hay need to be harvested and transported from higher distances which increases costs of restoration significantly. The use of agriculturally produced hay-bales can only be a compromise if no other material is available, because of the uncertain composition

and often low amount of target diaspores. In the case of suitable technical and financial conditions and/or available local hay sources, the restoration with plant material transfer can be a fast and effective method for restoration. If there is a sufficient budget the mentioned methods can be combined each other or with topsoil removal, which can greatly enhance the success but raise the costs.

We found that in most cases the use of low diversity seed mixtures composed by native grasses and yearly mowing enabled the recovery of basic grass diversity and was promising in weed suppression. It was revealed that short-lived weed assemblages can be easily suppressed; however, the composition of the seed mixtures can strongly influence the success where perennial clonally spreading weeds are typical. In such cases the sowing of clonally spreading competitor grasses may favour the weed suppression. We found that the increased level of biomass production is beneficial for the suppression of early weedy forbs. At the same time, the increased levels of litter and graminoid biomass can also hamper the establishment of several characteristic grassland species by competitive exclusion and/or by decreasing gap availability. To facilitate the development of a natural species composition typical in target native grasslands, the reduction of litter and graminoid biomass may be necessary. Several studies suggested that the recovery of low levels of nutrients characteristic to native grasslands in restoration sites can last several decades. Therefore, introducing traditional levels of management characteristic to native grasslands may not be the most appropriate option to decrease biomass in sites with improved productivity. 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). In spite of yearly mowing and the rapid recovery of sown grass' cover, still a dense persistent weed seed bank is present in the soil of most fields. This fact points out that high intensity grazing and/or trampling should be avoided, especially in the first years after the sowing.

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Country	Grassland and burning type	Positive effects of burning	Negative effects of burning	Recommendations	Reference
Estonia	floodplain meadow, early spring burning, 4 times (within a 6 years' time)	reduction of litter, prevention of woody encroachment	species richness did not increase, contrary to mowing and mulching treatments	burning is not recommended	Liira et al. 2009
Germany	calcareous grassland, yearly winter burning (25 years)	reduction of litter, prevention of woody encroachment	species composition was similar to that of fallow plots, cover of <i>Brachypodium pinnatum</i> increased	burning is not recommended	Kahmen et al. 2002; Moog et al. 2005
	meadow-like grassland, late winter burning (1 year)	warmer and drier microclimate, delayed spread of existing trees	decline of snail individuals, the elimination of woody species was not complete	burning is recommended	Page et al. 2004
	meadow-like grassland, late winter burning twice within a 4 years' time	most of the target species were not sensitive to burning	elimination of woody species and <i>Solidago gigantea</i> was not complete with solely burning	burning is feasible jointly with grazing or shrub clearance	Rietze 2009
Netherlands	dry dune grasslands, winter burning (1 year)	-	burning was not successful in nutrient removal	burning is feasible jointly with grazing	Vogels 2009
Sweden	commercial hayfield, early spring burning (1 year)	reduction of litter	species composition was similar to that of fallow plots	burning is not recommended	Antonsen et al. 2005
	semi-natural pasture, yearly early-spring burning (15 years)	reduction of litter	species richness declined, cover of tall herbs increased, untargeted species composition	burning is not recommended	Hansson et al. 2000
	semi-natural grassland, yearly early spring burning (28 years)	-	species richness declined, untargeted species composition	burning is not recommended	Wahlman et al. 2002
Switzerland	limestone grassland, yearly winter burning (22 years)	increased cover of several rare species	species richness declined, cover of <i>B. pinnatum</i> increased	burning is not recommended	Köhler et al. 2005
	limestone grassland, yearly winter burning (15 years)	reduction of litter	species richness declined, cover of <i>B. pinnatum</i> increased	burning is not recommended	Ryser et al. 1995

Table 2. Major characteristics of grassland restorations using high-diversity (HD) and low-diversity (LD) seed mixes and spontaneous succession.

Restoration technique	Accessory technique	Number of sown species	Sowing density (kg/ha)	Establishment success (species numbers)	Reference
HD seed mix	ploughing / grazing or mowing	14	20	13 sown, 6 unsown species (year 1); 4 / 3 (year 6)	Warren et al 2002; Fig. 1
spontaneous succession	ploughing / grazing or mowing	none	none	6 unsown species (year 1); 4 sown, 14 unsown species (year 6)	Warren et al 2002; Fig. 1
HD seed mix	ploughing / mowing and grazing	25-41	25-28	15.8 sown, 10.6 unsown species (year 1); 16.9 / 5.0 (2 year); 16.8 / 4.5 (year 3); 17.2 / 4.7 (year 4)	Pywell et al 2002; Table 5
LD seed mix	ploughing / mowing and grazing	6-17	25-31	6.1 sown, 10.0 unsown species (year 1); 6.6 / 4.2 (year 2); 7.5 / 4.4 (year 3); 8.9 / 5.0 (year 4)	Pywell et al 2002; Table 5
spontaneous succession	ploughing / mowing and grazing	none	none	1.1 sown, 9.3 unsown species (year 1); 3.2 / 8.0 (year 2); 5.2 / 9.8 (year 3); 7.8 / 10.8 (year 4)	Pywell et al 2002; Table 5
HD seed mix	ploughing and harrowing / mowing	27	20	7 sown grass species with 55% cover; 19 sown herbs with 30% cover	Jongepierová et al 2007; Fig. 2
spontaneous succession	ploughing and harrowing / mowing	none	none	perennial weeds 58% cover, 80 unsown grassland species with <5% cover	Jongepierová et al 2007; Fig. 2
HD seed mix	mowing (several regimes)	18	40	15 sown species; 34 or 40 non-sown species	Lawson et al 2004; Table 3
HD seed mix	harrowing / mowing	15	3500 seeds/m ²	10 unsown species (CZ); 2 (NL); 7 (SE); 5 (ES); 3 (UK)	Lepš et al 2001; Fig. 1
LD seed mix	harrowing / mowing	4	3500 seeds/m ²	9.5 unsown species (CZ); 5 (NL); 7.5 (SE); 6.5 (ES); 5 (UK)	Lepš et al 2001; Fig. 1
spontaneous succession	harrowing / mowing	none	none	15 unsown species (CZ); 12 (NL); 12.5 (SE); 9 (ES); 9 (UK)	Lepš et al 2001; Fig. 1
HD seed mix	ploughing/-	16	44.6	12 sown species	Owen & Marrs 2000

Table 2. continued.

Restoration technique	Accessory technique	Number of sown species	Sowing density (kg/ha)	Establishment success (species numbers)	Reference
spontaneous succession	harrowing / mowing	none	none	3 sown, 16 unsown species (CZ); 11 / 18 (NL); 3 / 28 (SE); 2 / 45 (ES); 5.5 / 33 (UK)	Lepš et al 2007; Fig. 2
HD seed mix	harrowing / mowing	15	3500 seeds/m2	10 sown, 12 unsown species (CZ); 12 / 10 (NL); 4.5 / 24 (SE); 3.5 / 29 (ES); 9.5 / 10 (UK)	Lepš et al 2007; Fig. 2
LD seed mix	harrowing / mowing	4	3500 seeds/m2	6 sown, 15 unsown species (CZ); 10 / 12 (NL); 2.5 / 26 (SE); 2 / 30 (ES); 6.5 / 22 (UK)	Lepš et al 2007; Fig. 2
HD seed mix	none / mowing and grazing	23	40	34 target, 45 total species	Manchester et al 1999; Table 2a
LD seed mix	none / mowing and grazing	4 or 11	40	19 target, 28 total species (4-species mix) or 27 / 37 (11-species mix)	Manchester et al 1999; Table 2a
spontaneous succession	none / mowing and grazing	none	none	21 target, 28 total species	Manchester et al 1999; Table 2a
HD seed mix	ploughing and harrowing / mowing	1, 2, 4, 8, 12, or 16	sown density increasing with diversity	0.5-1 target species (when 1 species sown); 1-2 (2); 3 (4); 5.5 (8); 8 (12); 6.5 (16)	Piper et al 2007; Fig. 4 (target)
LD seed mix	ploughing / mowing	4	30-35	4 sown species; 25 unsown species	Vécrin et al 2002; Fig. 1.
LD seed mix	ploughing / mowing, grazing	7	27	44 or mean 33 species (year 10); 56 or mean 40 species (year 14)	Sendzikaitė & Pakalnis 2006; Fig. 4 and 5
LD seed mix	ploughing / mowing	2 or 3	20-25	2 or 3 sown species (years 1-3); unsown species: 33.5 (year 1); 16.5 (year 2); 13.3 (year 3)	Török et al 2010; Table 2
HD seed mix	topsoil removal / grazing	56	1; 4; 10; 40	20 target, 12 weed species (at 1 kg/ha); 27 / 8 (4); 30 / 7 (10); 32 / 2.5 (40)	Stevenson et al 1995; Fig. 4c, d
spontaneous succession	topsoil removal / grazing	none	none	7 target, 16 weed species	Stevenson et al 1995; Fig. 4c, d

Table 3. Major characteristics of grassland restorations in former croplands using plant material transfer.

Target habitat type	Accessory technique	Number of species present in plant material	Amount of transfered plant material/ density of viable seeds	Establishment success (species numbers or transfer rate)	Reference
wet fen meadow	topsoil removal /none	species of fen meadows	in a thin layer of 5-10cm (ratio 1:1)	16 target, total 57 species/6 years	Patzelt et al 2001; Table 1
species rich calcareous grassland	topsoil removal (in some cases)/ moving and sheep grazing	54-78 potentially transferable species	231-805g hay/m ² 349-1264 seeds/m ²	transfer rate: 69-89%	Kiehl et al. 2006
species-poor <i>Corynephorion</i> (sandy grassland) species-rich <i>Armerion elongatae</i>	none/none	37 and 46	cca. 2kg/m ² in a thin layer of 5-10cm	species rich site: 23-25; 19; 20-21; 19-23; 16-19 (years 1-2-3-4-6) species poor site: 11-1; 10; 8; 6; 8 (years 1-2-3-4-6)	Kirmer & Mahn 2001; Table 4.
species-rich flood meadow	topsoil removal /moving	potentially 74-97 species	in a thickness of 5-10cm	total 41-70 species	Hölzel & Otte 2003; Table 1.
fen meadow	topsoil removal /grazing	41 transferred fen meadow species	in a thicknes of 5-7cm, 740g/m ²	species richness increased from 5-10 (year 1) to 20-25 (year 4)	Klimkowska et al. 2010a
species-rich flood meadow	ploughing/adding species poor grass seed mix (4 species; 5g/m ²)	-	a thickness of 10-15cm	between 23 and 95 species total 95 species	Donath et al. 2007

Table 4. Direct costs of various restoration measures. Generally costs for (i) plant material/seed, (ii) seed collection/plant material harvest/soil collection and/or removal, (iii) storage and transfer costs, (iv) site preparation (ploughing, disking, seed bed preparation), (v) sowing, spreading costs, (vi) some additional management costs (e.g. mowing, mulching or several additional techniques used in the first year of restoration) are included. Notations: HU = Hungary, UK = United Kingdom, CZ = Czech Republic, G = Germany, P =Poland, N =Netherlands.

Restoration technique		Targeted grassland type	Cost/ha in Euros	Reference	Region
Seed sowing	2-3 species, 25kg/ha	Alkali dry grasslands	225-465	Török et al. 2010, and (unpublished)	HU
	6-7 species, 25-31kg/ha	Species-rich neutral grassland	548	Pywell et al. 2002, and pers.comm.	UK
	6-17 species, 20-25kg/ha	Species-rich calcareous grassland	354	Pywell et al. 2002, and pers.comm.	UK
	6 species, 25kg/ha	Species-rich acid grassland	326	Pywell et al. 2002, and pers.comm.	UK
	4 species, 40kg/ha	Lowland wet meadows	185	Manchester et al. 1995	UK
	11 species, 40kg/ha	Lowland wet meadows	745	Manchester et al. 1995	UK
	23 species, 40kg/ha	Lowland wet meadows	1341	Manchester et al. 1995	UK
	15 species, 25kg/ha	Loess dry grasslands	375-520	Török et al. unpublished	HU
	39 species, 28kg/ha	Species-rich neutral grassland	1300	Pywell et al. 2002 and pers.comm.	UK
	41 species, 28kg/ha	Species-rich calcareous grassland	1927	Pywell et al. 2002 and pers.comm.	UK
	25 species, 25kg/ha	Species-rich acid grassland	1165	Pywell et al. 2002 and pers.comm.	UK
	30 species, 20kg/ha	Dry calcareous hay meadows	800-1000	Jongepierová et al.2007, and pers. comm.	CZ

Table 4. continued.

Restoration technique		Targeted grassland type	Cost/ha in Euros	Reference	Region
Plant material transfer	Plant material have to be bought	Loess dry grasslands	3240-3300	Török et al. unpublished	HU
	Own harvest, applied after storage of 3 months	Loess dry grasslands	595-650	Török et al. unpublished	HU
	Own harvest without storage (fresh material)	Loess dry grasslands	250-300	Török et al. unpublished	HU
	Own harvest without storage	Species rich floodplain meadow	6020-7763	Harnish & Donath unpublished	G
	Own harvest without storage, one mulching incl.	Species rich floodplain meadow	1800-8800	Donath et al. 2007	G
	Own harvest without spreading cost	Fen meadow	425	Klimkowska et al. 2010a	P
	Own harvest and transfer of heather shoots	Lowland heath/acid grassland	545	Pywell et al. 1995, and pers.comm.	UK
	Transfer of threshed hay	Various type of grasslands	6000-16000	Kirmer & Tischew 2006	G
	Topsoil removal and soil transport	Fen meadow (on organic soil)	16700	Klimkowska et al. 2010b	P
Topsoil removal	Topsoil removal without transport	Fen meadow (on organic soil)	13000	Klimkowska et al. 2010b	P
	Topsoil removal without transport	Various type of grasslands	4000-6000	Klimkowska pers. comm.	N
				Pywell et al. 1995 and pers.comm.	
Community translocation	With shallow soil layers	Lowland heath/acid grassland	14982		UK
	With deep soil layers	Wet moorlands and grasslands	1900000-3000000	Kirmer & Tischew 2006	G

Table 5. Correlation coefficients (r) between species richness and biomass of herbaceous group and the amount of litter and sown grass biomass 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: A1-4: Alkali seed mixture restored fields, L1-6: Loess seed mixtures restored fields.

	Field codes	p	Sown graminoid biomass	p	Litter
Forb biomass	A1	***	-0.62	***	-0.75
	A2	**	-0.51	**	-0.65
	A3	*	-0.43	***	-0.64
	A4	n.s.	-0.17	***	-0.63
	L1	n.s.	0.17	*	-0.45
	L2	***	-0.66	***	-0.84
	L3	n.s.	-0.18	***	-0.64
	L4	n.s.	-0.32	**	-0.56
	L5	*	-0.37	***	-0.66
	L6	*	-0.41	***	-0.59
	A1	***	-0.71	***	-0.80
	A2	**	-0.47	***	-0.67
Forb species richness	A3	*	-0.37	***	-0.71
	A4	n.s.	-0.17	***	-0.67
	L1	n.s.	0.31	n.s.	-0.37
	L2	***	-0.67	***	-0.85
	L3	n.s.	-0.12	***	-0.65
	L4	n.s.	-0.35	**	-0.55
	L5	*	-0.38	**	-0.57
	L6	**	-0.53	**	-0.57

Table 6. Species richness and cover scores of short lived-weeds and cover (mean \pm SE, %) of sown grasses in fields sown with alkali and loess seed mixtures. Different superscripted letters indicate significant differences between years (RM ANOVA and Tukey test, $p < 0.001$, $N=9$ for alkali, and $N=8$ for loess fields, respectively).

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

Table 7. Mean cover scores of frequent species detected in sown fields in Year 1, Year 2 and Year 3 (species with a mean cover of at least 5% in at least one field were listed). Weeds were indicated with **boldface**. Field codes: seed mixture: A – alkali, L – loess, followed by field number. **FSG** – functional species groups: S – short-lived, P – perennial, F – forb, G – graminoid.

Year 1	F	A1	A2	A3	A4	L1	L2	L3	L4	L5	L6
<i>Bromus arvensis</i>	S	3.5	2.4	4.3	16.					0.1	0.3
<i>Bromus inermis</i>	P					2.1	1.4	0.5	25.	2.5	0.7
<i>Bromus mollis</i>	S	1.2	2.0	1.5	12.	1.3	0.2	0.3	4.0	0.5	0.8
<i>Capsella bursa-pastoris</i>	S	32.	10.	2.4	3.3	11.	2.9	4.0	31.	19.	18.
<i>Consolida regalis</i>	S								0.4	6.3	0.7
<i>Fallopia convolvulus</i>	S	1.4					0.7	0.3		15.	29.
<i>Festuca pseudovina</i>	P	1.1	0.6	10.	11.						
<i>Fumaria officinalis</i>	S	0.6						0.2		9.8	27.
<i>Lamium amplexicaule</i>	S	1.4	0.2		0.1		0.2	0.4	0.1	7.3	4.8
<i>Matricaria inodora</i>	S	0.2	12.	18.	24.	60.	78.	50.	25.		
<i>Papaver rhoeas</i>	S									9.8	
<i>Poa angustifolia</i>	P	0.8	54.	39.	22.	17.	3.9	0.1	6.5	1.2	0.6
<i>Polygonum aviculare</i>	S	46.	13.	10.	3.1	0.3	0.9	16.	1.3	8.4	6.6
<i>Stellaria media</i>	S	1.3	0.9		3.2	0.5	6.2	22.		0.2	

Year 2	F	A1	A2	A3	A4	L1	L2	L3	L4	L5	L6
<i>Agropyron sp.</i>	P	11.	10.		12.			13.			2.0
<i>Bromus inermis</i>	P					40.	27.	44.	71.	27.	55.
<i>Bromus mollis</i>	S	11.	1.7			0.1	1.1	2.0	0.1	3.7	2.7
<i>Capsella bursa-pastoris</i>	S	32.	5.0								1.8
<i>Convolvulus arvensis</i>	P	0.2	0.1	0.1	0.7		0.4	0.1	0.9		16.
<i>Festuca pratensis</i>	P	0.2		1.3	5.9						
<i>Festuca pseudovina</i>	P	7.9	40.	10.	44.						
<i>Festuca rupicola</i>	P					4.9	8.2	14.	4.2	51.	9.6
<i>Matricaria inodora</i>	S	11.	1.0	0.1		0.9	0.4	0.1			0.6
<i>Poa angustifolia</i>	P	20.	39.	86.	33.	45.	48.	24.	23.	10.	2.6
<i>Vicia villosa</i>	S				0.1	5.4	0.5				

Table 7. continued.

Year 3	F	A1	A2	A3	A4	L1	L2	L3	L4	L5	L6
<i>Agropyron sp.</i>	P	52.	24.		7.2			3.4			6.1
<i>Bromus inermis</i>	P					15.	24.	33.	46.	33.	9.7
<i>Bromus tectorum</i>	S	6.3			0.1			0.1		1.2	0.3
<i>Convolvulus arvensis</i>	P	0.5	0.3		0.5		0.1	0.7	1.5		13.
<i>Festuca pseudovina</i>	P	16.	30.	15.	47.						
<i>Festuca rupicola</i>	P					47.	30.	14.	27.	52.	60.
<i>Poa angustifolia</i>	P	18.	44.	72.	31.	29.	24.	39.	16.	9.4	1.9
<i>Trifolium striatum</i>	S						7.8	0.0	1.1		
<i>Vicia hirsuta</i>	S	0.2		7.8	5.1	1.4	3.4	1.2	4.5		1.3

Table 8. Mean cover proportions of frequent species detected in reference grasslands (species with a mean cover of 5% in at least one grassland were listed). Weeds were indicated with **boldface** (based on Grime 1979 and Borhidi 1995). Notations: AG1-3: alkali grasslands, LG1-3: loess grasslands.

	FSG	AG1	AG2	AG3	LG1	LG2	LG3
<i>Trifolium campestre</i>	SF	5.4	5.0	1.4			
<i>Vicia hirsuta</i>	SF				10.9	2.9	2.5
<i>Achillea collina</i>	PF	12.9	3.3	14.5			
<i>Achillea setacea</i>	PF		7.5				
<i>Convolvulus arvensis</i>	PF				2.1	7.9	3.7
<i>Galium verum</i>	PF				0.1	5.4	3.5
<i>Lathyrus tuberosus</i>	PF					6.5	2.3
<i>Plantago lanceolata</i>	PF	12.0	9.0	3.8			
<i>Salvia nemorosa</i>	PF				50.0	36.3	20.5
<i>Bromus inermis</i>	PG				32.5	53.8	58.8
<i>Carex praecox</i>	PG				7.3	3.5	0.1
<i>Festuca pseudovina</i>	PG	50.0	65.5	57.5			
<i>Festuca rupicola</i>	PG				3.1	6.3	2.0
<i>Poa angustifolia</i>	PG				2.8	3.7	5.8

Table 9. Mean seed bank density scores of frequent species and total seed density detected in seed banks of the sown fields (species detected with at least 30 viable seeds total are listed). Weeds were indicated with **boldface** (based on Grime 1979 and Borhidi 1995). One seedling recorded in the samples of a certain field corresponds with a seed density of 66 seeds per m².

Species	A1	A2	A3	A4	L1	L2	L3	L4	L5	L6
<i>Amaranthus retroflexus</i>	332	66		464		133		199		133
<i>Capsella bursa-pastoris</i>	3647	4708	2719	3183	4377	4974	6234	6963	10345	5106
<i>Chenopodium album</i>	2984	597	133	1592	199	398	1525	928	398	4443
<i>Cirsium arvense</i>									66	
<i>Conyza canadensis</i>	66	199	663	928	1194	66	265	66	199	133
<i>Echinochloa crus-galli</i>		199	398	66		133	199	199	332	
<i>Epilobium tetragonum</i>	66	796		133		66	66	133		
<i>Festuca pseudovina</i>	66	133		199						
<i>Gypsophila muralis</i>		332	6499	729			133	928		
<i>Lamium amplexicaule</i>	199	199				531	133		265	66
<i>Lepidium campestre</i>				2321			133	66		
<i>Matricaria chamomilla</i>		1857	1989	199						
<i>Matricaria inodora</i>	133	597	1260	1857	332	1260	1260	265	66	199
<i>Poa angustifolia</i>	531	1260	265	199	265	265	796		332	133
<i>Polygonum aviculare</i>	1061	729	862	796		133	199	66	995	464
<i>Setaria glauca</i>		133			1658	3714	3714			
<i>Setaria viridis</i>						199	663		1790	1525
<i>Spergularia rubra</i>			4642		663		66	199		
<i>Stellaria media</i>	663	66		1592	265	862	1459			
<i>Thlaspi arvense</i>	66	332	66	133	66	332	1127	265	1724	
<i>Typha sp.</i>	2321	2122	597	1194	199	265	265	729	265	729
Total seed density	14523	15120	22215	16512	9417	13860	18833	11141	18568	15053

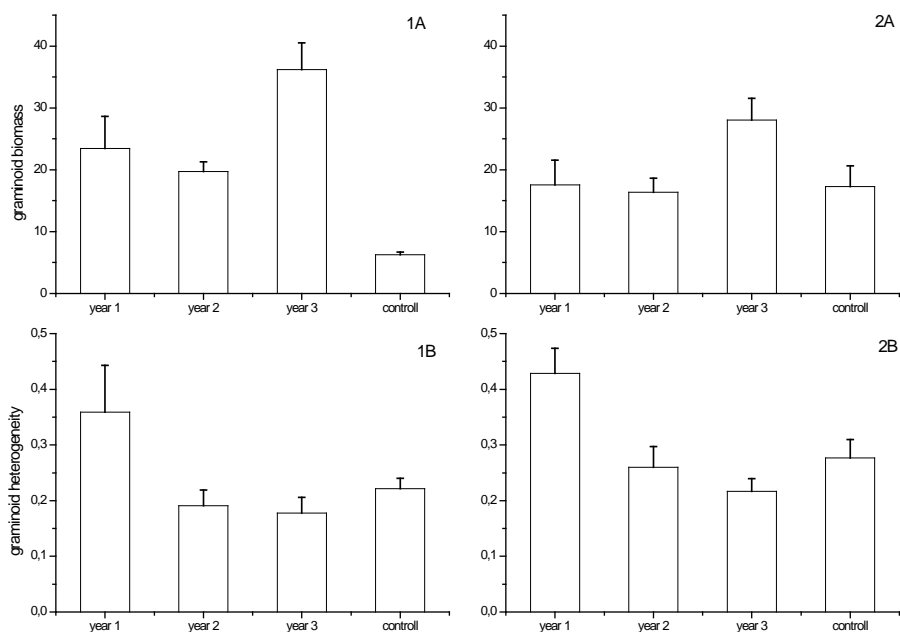


Fig. 1. Biomass (A) and biomass heterogeneity (B) scores of graminoids in alkali seed mixtures (1), and loess seed mixtures (2) sown fields (mean \pm SE). Scores for native grasslands are shown in the last column in every subfigure (in 1A and 1B subfigure scores for alkali, in 2A and 2B scores for loess native grasslands are shown).

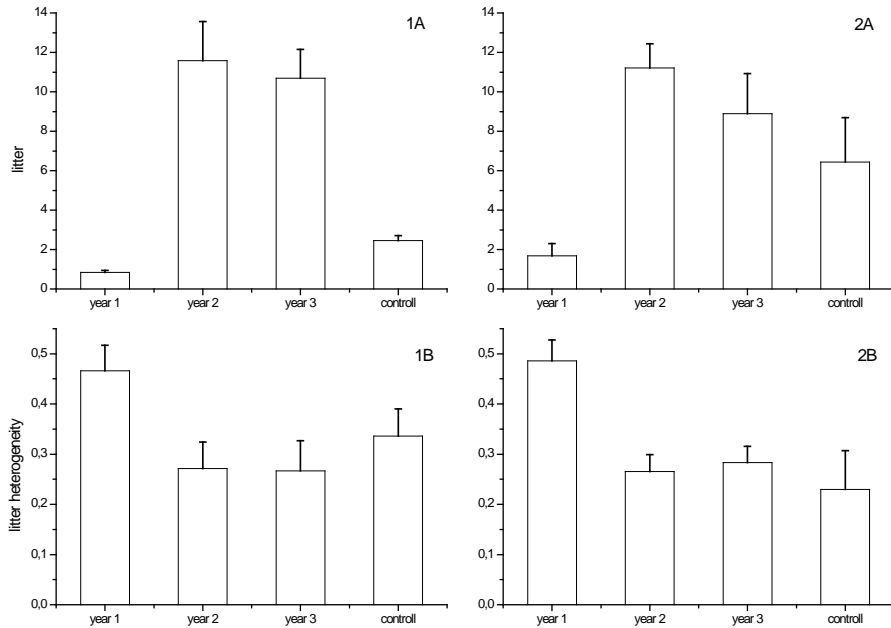


Fig. 2. Litter (A) and litter heterogeneity (B) scores for graminoid biomass in alkali seed mixtures (1), and loess seed mixtures (2) sown fields (mean \pm SE). Scores for native grasslands are shown in the last column in every subfigure (in 1A and 1B subfigure scores for alkali, in 2A and 2B scores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