In: Seed Banks: Types, Roles and Research ISBN: 978-1-53610-388-5
Editor: Janice Murphy 

*Chapter 1*

# SEED BANK RESEARCH IN CENTRAL-EUROPEAN GRASSLANDS- AN OVERVIEW

***Réka Kiss*[1], *Orsolya Valkó*[2], *Béla Tóthmérész*[2] *and Péter Török*[1,*]**

[1]Department of Ecology, University of Debrecen, Debrecen, Hungary
[2]MTA-DE Biodiversity and Ecosystem Services Research Group, Debrecen, Hungary

## ABSTRACT

Seed banks represent an important, but largely undiscovered and underappreciated component of grassland vegetation dynamics. Given its importance, our aim was to provide a comprehensive overview about the current study of seed banks in Central-European grasslands by a literature review. We found in total 32 studies about seed banks of Central-European grasslands, with a majority of studies originating from Poland, Germany and Hungary. Most studies used the seedling emergence method in seed bank analyses. Disturbed grasslands contained a higher seed density and higher number of persistent species than undisturbed ones. The similarity between the species composition of aboveground vegetation and seed banks was generally low to medium, but in some cases high similarity was also found (Sørensen similarity between 0.13-0.75). In disturbed grasslands not only the seed density and species richness, but also the similarity with aboveground vegetation was higher

[*] Corresponding Author address; Email: molinia@gmail.com.

than in undisturbed ones. Studies noted an increase in seed density and species richness in the course of succession and also noted the highest values at the end of the so-called mid-successional stage. Studies agreed that seed bank alone is not enough for habitat restoration so interventions and continuous management is necessary for successful restoration. The seed bank contained seeds of annuals and short-lived species, but the characteristic grassland specialists generally lacked from the seed bank, thus there is a need for their active introduction in most cases.

**Keywords**: Central-Europe, grassland, management, seed bank, succession, restoration

## 1. Introduction

Grasslands are vital elements of Central-European landscapes and harbour an extraordinarily high number of endangered plant and animal species (Dengler et al. 2014, Valkó et al. 2016a). There are several biodiversity hotspots in Central-Europe, out of which the Carpathian mountain range harbour sites with world records of vascular plant species richness. For example, in the White Carpathians, as many as 109 vascular plant species were found in a 4×4-m plot (Chytrý et al. 2015, Wilson et al. 2012). Besides these biodiversity hotspots, the species richness of Central-European grasslands is declining in many areas because of landscape-scale changes in land use, management intensity and human development (Valkó et al. 2012). The rate of conversion of natural ecosystems to croplands or urban areas is increasing (Deák et al. 2016), but parallel the abandonment of marginal croplands is also became typical in many regions (Valkó et al. 2016b). These dynamic landscape-scale changes all influence both the diversity and species composition of pristine and degraded grasslands. The establishment of a respective plant species can in a particular site largely depends on their persistence traits, such as the ability to build up persistent soil seed banks. Thus, studies on the soil seed banks of Central-European grasslands help to predict the response of grassland ecosystems to dynamic landscape-scale changes and help site managers and researchers to evaluate degradation and regeneration processes.

Reproduction by seeds is characteristic to almost all vascular plants. Most seeds germinate shortly after maturation and dispersal. In contrast, species also produce seeds which do not germinate after the dispersal despite the favourable conditions and remain dormant in the soil for a longer period of time. In case of non-dormant seeds secondary dormancy can also be induced by unfavorable conditions, such as burial. These seeds form the persistent soil seed bank. Depending how much time viable seeds spend in the soil three categories were proposed by Thompson et al. (1997). Seeds that remain viable less than a year form the transient seed bank category. The seeds that remain viable till five years possess short-term persistent seed banks and species with viability longer than five years have long-term persistent seeds. Species have different strategies of forming seed banks. Some species produce many small seeds with a long viability but in contrast there are others which prefer clonal growth so they do not produce seeds at all or only small number of large but transient seeds. The potential of species to produce seeds depends also on the habitat type. Species of frequently disturbed habitats (e.g., short-lived weed species) tend to produce many persistent seeds. The seed bank of a habitat can be very different from the apparent vegetation (Bossuyt andHonnay 2008, Koncz et al. 2011), because in more persistent habitats like forests there are more species producing larger seeds in less numbers and shorter viability (Matus et al. 2005, Bossuyt andHonnay 2008).

The study of seed banks provides information about the past management practices and their impact on the current and future vegetation (Valkó et al. 2011). The seed bank also provides information about the former and apparent levels of degradation (Hong et al. 2012) and has a decisive role in the temporal dispersion of species contributing to the conservation of the genetic variability of plant populations (Hong et al. 2012). It may also have a role in habitat restoration which topic is in the mainstream of seed bank studies. Most results suggest that the seed bank has a limited importance in habitat restoration processes and successful restoration needs propagule imput (McDonald 1993, Blomqvist et al. 2003, Rosef 2008, Stroh et al. 2012). Other studies claim that seed banks may have role in the habitat restoration but spontaneous recovery requires long time (Plassmann et al. 2009, Wang et al. 2010).

## 2. Aims of the Study

Our aim was to review the seed bank studies conducted in Central-European grasslands. We searched for the English papers available online in Thomson's Web of Science, published between 1990-2015, using the keywords "seed bank" AND "grassland OR meadow OR field" and the search were filtered to the countries in Central Europe. We browsed the abstracts and selected those papers, in which complete seed banks and their changes in relation to different management types, habitats, successional stages and also their role in restoration were studied After the selection we found 32 studies which matched the criteria.

## 3. RESULTS

We found 1 publication from Austria, 1 from Switzerland, 5 from the Czech Republic, 8 from Germany, 8 from Hungary and 9 from Poland. We found no publications fitting our criteria from Liechtenstein, Slovakia and Slovenia (Figure 1).

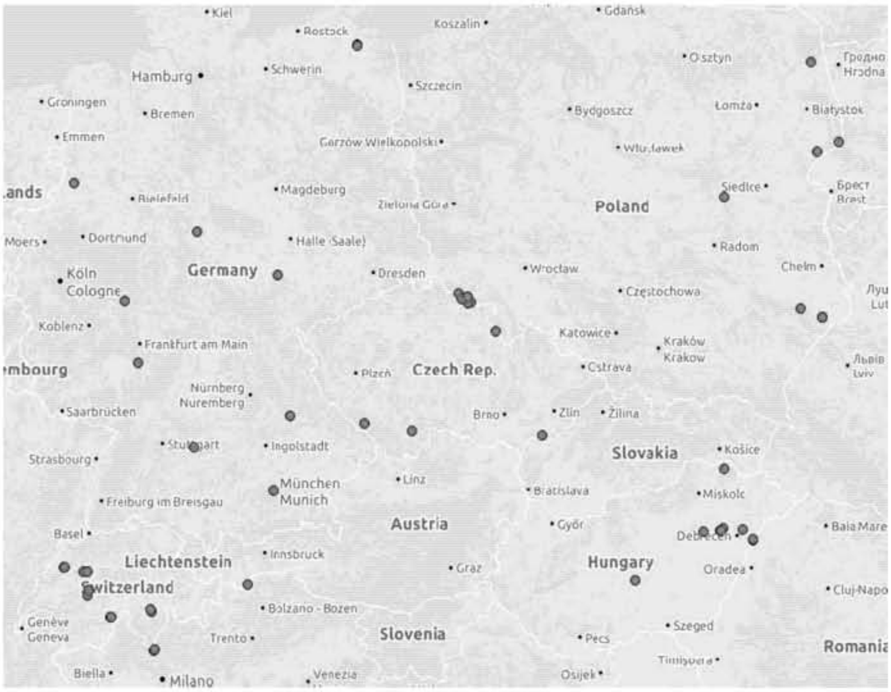


Figure 1. Locations of the Central-European seed bank studies. Note that the number of locations is not equal to the number of studies (some studies had the same locations, others had multiple locations).

## 3.1. Method Selection

Most of the studies, numerically 23 studies, used the seedling emergence method in greenhouse for seed bank analysis (Bekker et al. 1997, Stroh et al. 2002, Matějková et al. 2003, Matus et al. 2003, 2005, Handlová and Münzbergová 2006, Wagner et al. 2006, Wellstein et al. 2007, Dölle and Schmidt 2009, Klimkowska et al. 2009, Marcante et al. 2009, Török et al. 2009, 2012, Albrecht et al. 2011, Kwiatkowska-Falińska et al. 2011, Valkó et al. 2011, 2014, Klimešová et al. 2013, Karlík and Poschlod 2014, Tóth and Hüse 2014, Zeiter et al. 2014, Franczak and Czarnecka 2015, Havrdová et al. 2015) but seedling emergence in growth chambers was also used (Kemény et al. 2005). However, we also found that in some studies the seed bank was determined using the seed extraction method. In these studies all seeds were counted and no viability tests were done (Czarnecka 2005, 2008). Some of the studies used multiple methods not only for comparing their usefullness and results but also for the best knowledge of seed bank (Falińska 1998, 1999, Czarnecka 2004a, b, Weiterová 2008, Koch et al. 2011). These latter studies generally used the seed extraction method combined with the seedling emergence method. In the seed extraction method researchers separated the seeds by extraction from the soil samples and then used a binocular microscope for seed counting. After the separation they used the seedling emergence method in greenhouse for viability testing; the seedlings were counted, identified and then removed.

The most significant difference found in these studies was that the seed extraction method generally overestimated the seed bank density compared to the seedling emergence method and also found a higher similarity with aboveground vegetation (Falińska 1998, 1999, Weiterová 2008, Koch et al. 2011). Koch et al. (2011) was able to detect species with the seedling emergence method, which were not detected with seed extraction method.

## 3.2. Species Diversity, Seed Density and Similarity of Seed Bank with Vegetation

Taking into acount only the studies analyzing the 10cm depth of soil, the papers found similar species diversity in grasslands. Alkaline grasslands hosted 17-36 species/5,670cm$^3$ (Valkó et al. 2014) while loess grasslands had 44-52 species/4,536cm$^3$ (Tóth and Hüse 2014). In sand grasslands 33-37 species/3,140cm$^3$ (Matus et al. 2003), 32-51 species/3,770cm$^3$ (Matus et al.

2005) and 35-45 species/3,770cm$^3$ (Török et al. 2009) species were found. Subalpine pastures had 36 species/50,240cm$^3$ (Marcante et al. 2009). The species density of calcareous grasslands ranged between 16-37 species/6,300cm$^3$ (Karlík and Poschlod 2014).

The available seed bank density intervals of studied habitats are listed in Table1. Weiterová (2008) found in oligothrophic wet meadows 25,124 seed/m$^2$/10cm mentioning, that this is the total seed bank found but the number of undamaged seeds is only the half of it (12,031 seeds/m$^2$/10cm). Czarnecka (2004b) studied short-term successional changes in mesophilous grassland dominated by *Brachypodium pinnatum, Aster amellus* or *Senecio macrophyllus*. She found that seed densities increased from 2,482 to 3,128 seeds/m$^2$/5cm in *Brachypodium pinnatum* grasslands and from 3,772 to 4,199 seeds/m$^2$/5cm in *Aster amellus* grasslands and decreased from 15,934 to 10,132 seeds/m$^2$/5cmin *Senecio macrophyllus* grasslands in the first three years of succession. In *Cirsio–Brachypodion pinnati* grassland the seed bank ranged between 7,174-14,121 seeds/m$^2$/5cm (Czarnecka 2005, Czarnecka 2008). Contrary to these high values using the same method Falińska (1998) and (1999) detected only 2,975-7,915seeds/m$^2$/3cm in *Cirsietum rivularis* meadows.

Using seedling emergence method the lowest soil seed density was found along a primary succession in glacier forelands (Marcante et al. 2009). The seed bank ranged between 273seeds/m$^2$/5cm in the initial stage and 3,674seeds/m$^2$/10cmin subalpine pastures representing old succession stages. In xerothermic grasslands Czarnecka (2004b) found low seed densities, which further decreased (not every case significantly) in course of the three study years from 675 to 522 seeds/m$^2$/5cm in *Brachypodium pinnatum* grassland, from 1,575 to 1,485 seeds/m$^2$/5cm in *Aster amellus* grassland and from 5,283 to 3,798 seeds/m$^2$/5cm in *Senecio macrophyllus* grassland. Low values were also detected in *Brachypodium pinnatum* dominated dry-mesophylous grasslands (Valkó et al. 2011) where seed density ranged between 4,350-6,339 seeds/m$^2$/10cm. Waterlogging caused by beavers dam building initiated seed density changes in wet meadows, where the soil seed bank density increased from 3,768 to 3,858 seeds/m$^2$/5cmin three years. In similar meadow without waterlogging a decrease from 5,087 to 4,536 seeds/m$^2$/5cm was detected (Franczak and Czarnecka 2015). The seed bank of acidic sand grasslands ranged in a larger interval, between 10,300-40,900 seeds/m$^2$/10cm(Török et al. 2009). Matus et al. (2003) found 11,240-15,950 seeds/m$^2$/10cmand similarly 13,900 seeds/m$^2$/10cm in unmanaged sandy grassland and 24,600 seeds/m$^2$/10cmin grazed grasslands (Matus et al. 2005). The seed density of

58-3,155 seeds/m$^2$/5cmfound in calcareous sand grasslands by Kemény et al. (2005) was very low compared to previous values. Mesic grasslands contained a seed bank between 9,460-11,513 seeds/m$^2$/10cm depending on the management applied (Wellstein et al. 2007). Seed bank of degraded calcareous grasslands ranged between means of 11,908-14,505 seeds/m$^2$/10cm between 2000 and 2002 (Wagner et al. 2006). Karlík and Poschlod (2014) found even lower soil seed bank densities ranging between 2,523 and 5,457seeds/m$^2$/10cm. Alluvial meadows had a seed density of 17,060 seeds/m$^2$/10cm (Havrdová et al. 2015). Loess grasslands (20,200-22,800 seeds/m$^2$/10cm: Tóth and Hüse 2014) and limestone grasslands (17,628-49,720 seeds/m$^2$/20cm: Koch et al. 2011) had similar soil seed bank density scores. Alkaline grasslands had a slightly higher seed density of 30,104-51,410 seeds/m$^2$/10cm (Valkó et al. 2014). Highest seed density was detected in fen meadows by Valkó et al. (2011): 63,980-94,034 seeds/m$^2$/10cm.

The similarity of seed bank with vegetation was the lowest in case of restored former agricultural lands, where in the first year after sowing alkali and loess seed mixtures the Jaccard similarity was 0.38 and in three years decreased to 0.16 due to the supression of weed species from vegetation but their significant contribution to the seed bank (Török et al. 2012). Using the same index a similarity between 0.20-0.44 was found in geese grazed sand grasslands (Török et al. 2009). In loess grasslands the similarity was 0.31-0.35 (Tóth and Hüse 2014) and in moist meadows slightly higher, 0.36-0.48 values were found (Franczak and Czarnecka 2015). Not grazed and overgrazed sand grassland had similarity values between 0.32-0.41 (Matus et al. 2005). Bossuyt and Honnay (2008) reported a mean Jaccard similarity of 0.48 in case of grasslands and mentioned that this habitat type had the highest similarity index. They also mentioned that there are big differences between grassland types, meadows and acid grasslands had the highest similarity and calcareous ones the lowest ones. Calculating Sørensen similarity, Havrdová et al. (2015) found low (0.13-0.17) similarity values in alluvial meadows abandoned from different period of time.

Valkó et al. (2011) found similarity of 0.28-0.36 in dry-mesophilous meadows, while the similarity of fen meadows was higher, ranging between 0.41–0.53. Alkali grasslands had similarity values of 0.37-0.47 (Valkó et al. 2014). The similarity of recently formed and old calcareous grasslands increased with time since last agricultural use and its values ranged between 0.29-0.57 (Karlík and Poschlod 2014). The similarity in limestone grasslands was 0.16-0.43 (Koch et al. 2011). Kemény et al. (2015) found very different similarity values depending on the sampling season. The similarity values were lower (0.29-0.56) in spring samples than in autumn samples (0.54-0.76). The average Sørensen's similarity index in grassland found by Hopfensperger (2007) was 0.54, which was higher than similarity found in case of forests and wetlands. These results are in accordance with results found by Bossuyt and Honnay (2008). She also found, that the similarity increased with the age of system, young systems having a lower similarity which increased gradually with the age of grasslands.

**Table 1. Seed bank densities in studied grasslands of Central-European countries. Countries are abbreviated as follows: A – Austria, CH-Switzerland, CZ- Czech Republic, D- Germany, H- Hungary, PL-Poland**

| Section | Grassland type | Density range (seed/m$^2$) | Depth (cm) | Number of studies | Country | Reference |
|---|---|---|---|---|---|---|
| 3.4.1.Lowland dry grasslands | | | | | | |
| 3.4.1.1. | Alkali grassland | 30,104-51,410 | 10 | 1 | H | Valkó et al. 2014 |
| 3.4.1.2. | Loess grassland | 20,200-22,800 | 10 | 1 | H | Tóth and Hüse 2014 |
| 3.4.1.3. | Sand grassland | 58-40,900 | 10 | 4 | H | Matus et al. 2003, 2005, Kemény et al. 2005, Török et al. 2009 |
| 3.4.1.4. | Limestone grassland | 17,628-49,720 | 20 | 1 | D | Koch et al. 2011 |
| 3.4.1.5. | Xerothermic grassland | 1,642-21,217 | 5 | 4 | PL | Czarnecka 2004a, b, 2005, 2008 |
| 3.4.2. Mountain dry grassland | | | | | | |
| 3.4.2.1. | Subalpine grasslands | 273-3,674 | 10 | 1 | A | Marcante et al. 2009 |
| 3.4.2.2. | Dry calcareous grassland | 2,523-5,457 | 10 | 1 | D | Karlík and Poschlod 2014 |
| 3.4.2.3. | Mesic grasslans | 9,460-11,513 | 10 | 1 | D | Wellstein et al. 2007 |
| 3.4.2.4. | *Festuco-Brometea* and *Arrhenatheretalia*-type grasslands | 1,695-25,116 | 2,5 | 1 | CH | Zeiter et al. 2014 |

| Section | *Grassland type* | Density range (seed/m2) | Depth (cm) | Number of studies | Country | Reference |
|---|---|---|---|---|---|---|
| 3.4.2.5. | Dry mesophylous grassland | 4,350- 6,339 | 10 | 1 | H | Valkó et al. 2011 |
| 3.4.3. Moist and wet grasslands | | | | | | |
| 3.4.3.1. | Fen meadow | 35,304-94,034 | 10 | 2 | H, PL | Valkó et al. 2011, Klimkowska et al. 2009 |
| 3.4.3.2. | Alluvial meadow | 17,060 | 10 | 1 | CZ | Havrdová et al. 2015 |
| 3.4.3.2. | *Lysimachio vulgaris-Filipenduletum* meadow | 3,768-5,087 | 5 | 1 | PL | Franczak and Czarnecka 2015 |
| 3.4.3.3. | *Cirsietum rivularis* meadow | 2,975-7,915 | 3 | 2 | PL | Falińska 1998,1999 |
| 3.4.4. Grasslands with anthrophogenic influence | | | | | | |
| 3.4.4.1. | Degraded grasslands | 2,230-14,505 | 20 | 2 | D | Wagner et al. 2006, Albrecht et al. 2011 |
| 3.4.4.2. | Secondary grasslands | 1,500-30,000 | 10 | 2 | CZ | Handlová & Münzbergová 2006, Kwiatkowska-Falińska et al. 2011 |

## 3.3. Vertical Distribution of Seeds

According to the general trend, seed bank is more dense and species-rich in the upper 0-5 cm soil layer (Blomqvist et al. 2003, Bossuyt et al. 2006, Plassmann et al. 2009, Wang et al. 2010). Most of studies are in agreement with the former assumption, but in some cases there were found inverse values. Marcante et al. (2009) explained the higher seed density of deeper 2-5 cm soil layer in pioneer stages of succession of alpine grasslands with the changes of soil structure because with time the upper soil layer also becomes more densely structured which prevents seeds from entering deeper soil layers. They also noticed the higher similarity of deeper soil layer with vegetation. In former arable fields yearly ploughing resulted in a higher seed density in soil layers deeper than 10 cm than in upper soil layer (soil seed bank inversion, Dölle and Schmidt 2009). Klimkowska et al. (2010) also found higher seed density in deeper 5-15 cm of fens and 5-10 cm of degraded fens. They explained their findings with the structure of soils in fens which enables seeds to easily enter to deeper soil layers and also with the unfavorable conditions of the topsoil for seed survival (e.g., extremly heated and dry soil). Short-lived weedy species and hygrophytes in some cases reached the highest seed densities in deeper soil layers (Török et al. 2009, Valkó et al. 2011).

## 3.4.Studied Habitats

### *3.4.1.Lowland Dry Grasslands*

#### 3.4.1.1.Alkali Grasslands

There was only one soil seed bank study in alkali grasslands, which considered not only the seed bank diversity and density, but also the effects of environmental parameters on it (Valkó et al. 2014). Three alkali grassland types were studied along a fine-scale elevation gradient in East Hungary. They found that besides elevation no other environmental parameter had an effect on seed bank density and diversity. The species composition of the grasslands was different, the similarity with the aboveground vegetation was generally low (0.37-0.47) and the seed bank consisted more species than the aboveground vegetation. One species, *Jucus compressuss* was the dominant soil seed bank species in all grassland types regardless of elevation (4,894-38,619 seeds/$m^2$). Only a few other species were recorded in considerable densities. Hygrophytes had the highest seed density scores in the less stressed habitats so to the lowest and highest elevations (Figure 2).

#### 3.4.1.2.Loess Grasslands

Tóth and Hüse (2014) studied the seed banks of natural and degraded loess grasslands in East Hungary. They concluded that degradation (resulted by human disturbance) has a positive, but not significant effect on soil seed bank density and richness. The similarity between the species composition of seed banks and aboveground vegetation was low (0.31-0.35). The graminoids which had high cover had only low-density seed bank with the exception of *Poa angustifolia*. This species possessed a high seed density (1,061 seeds/$m^2$) in the semi-natural loess grassland. Some species with low coverage values also had high seed density in the seed banks, but loess specialist species were sparse or totally absent (Figure 3).

Figure 2. Alkali grasslands in Hortobágy National Park, East-Hungary. Photos of Tamás Miglécz.

Figure 3. Loess grassland in Hortobágy National Park, East-Hungary. Photo of Tamás Miglécz.

#### 3.4.1.3. Sand Grasslands

Many studies were conducted in sand grasslands (Figure 4) of different countries, with a special emphasis on the comparison of degraded and pristine sandy vegetation. Matus et al. (2005) studied the seed banks of acidic sandy grasslands grazed by domestic geese in Hungary. Grazed sites had a higher species richness and seed density in seed bank compared to sites released from grazing pressure (Table1). *Rumex acetosella* was the dominant seed bank species regardless of management type. In the seed bank of grazed and reference sites seeds of hygrophyte species were also present with higher density and diversity in grazed sites, but they were missing from vegetation. Another study in geese grazed acidic sand grasslands found that the seed bank was dominated by few species (Török et al. 2009). The most frequent species were annuals and short-lived perennial dicots, but there were also few graminoids who built up dense seed banks mainly in upper soil layer. Hygrophytes represented a significant part of seed bank, mainly in deeper soil layers and they were missing from vegetation. The similarity between the species composition of seed banks and aboveground vegetation ranged from low to medium, overgrazed stands having a similarity of 41% while reference stands only 32%. The seed bank was more similar to former more degraded successional stages.

Matus et al. (2003) studied seed banks of sandy grasslands which where released from cattle grazing and others in the same time invaded by *Robinia pseudoacacia*. They found a decrease of seed density in the seed banks of these abandoned grasslands. In the abandoned grasslands no significant species loss was detected in the seed bank but the dominance structure changed considerably, tall, competitive species becoming dominant in expense of low species, similarly to the findings of Klimešová et al. (2013). In invaded fields the vegetation composition changed drastically and these changes were also detectable in the seed bank. Besides these facts after years of invasion seeds of grassland species (such as *Rumex acetosella, Verbascum phoeniceum, Potentilla arenaria*) were still present in the seed bank, thus they likely had long-term persistent seed banks.

Kemény et al. (2005) analyzed seed bank dynamics in two consecutive years of four calcareous sandy grassland patches in Hungary. Two of the four patches had a closed microhabitat and the other two an open microhabitat. The results showed the dominance of annual species in all patches and that the seed bank was formed by only a few species (such as *Arenaria serpyllifolia, Erigeron canadensis, Erophila verna, Silene otites*). The seed bank density was changed during the sampling periods showing a minimum in spring and a maximum is in autumn samples. However, annuals had similar seed density scores in both periods while perennials were the ones who occurred mainly in autumn samples. Accordingly, the similarity of species composition was higher between the aboveground vegetation and autumn seed bank compared to spring seed bank. They also detected a higher seed density of annuals than that of perennials in closed patches where dominant grasses preferred vegetative spreading and were missing from the seed bank.

Figure 4. Sand grasslands in Kiskunság National Park, Central Hungary (left) and the Mainzer Sand, Southwest Germany (right). Photos of Tamás Miglécz.

### 3.4.1.4. Limestone Grasslands

In their study, Koch et al. (2011) analyzed the seed banks of limestone grasslands with different vegetation composition and cover in Germany. For control they used a limestone grassland which was deforested and the management was restored in 1978. In this grassland the vegetation was unchanged over the 13 years of the study. The study also compared the seedling emergence and seed rinsing methods of seed bank analysis. They found that the seed rinsing method (sample concentration by sieving machine and seed extraction under binocular) detected higher amount of seeds in the seed bank and so the similarity in this case with vegetation was also higher. In contrast the seedling emergence method detected species that were not found with the other method. The majority of seed bank species were hemicriptophytes. One third of seeds from seed bank built up transient or short-term persistent seed banks, while the remaining species possessed long-term persistent seeds. The Sørensen similarity between soil seed banks and aboveground vegetation was similar in the oldest limestone grassland (0.40) and in the plots deforested and mown after the '90s (0.16-0.43). The similarity of seed banks of young managed plots with old limestone grassland plot was also low. The results showed that the development of seed banks is slower than the development of the vegetation of a typical limestone grassland.

### 3.4.1.5. Other Types of Xerothermic Grasslands

Czarnecka published several studies conducted in xerothermic grasslands. In the first study (Czarnecka 2004a) she analyzed xerothermic grasslands on lower elevations dominated by *Aster amellus* and the higher elevation dominated by *Brachypodium pinnatum*. Comparison of two vegetation types showed the dominance of only a few species in the seed bank. The average seed density of the two seed banks was similar (Table1) but the species composition differed. Some species were common in the sites and the seed of almost all species from vegetation were present in seed bank. The similarity between seed bank composition and aboveground vegetation was high. The seeds showed a clustered spatial structure. In a second study (Czarnecka 2004b) she analyzed three vegetation types. Besides the grasslands dominated by *Aster amellus* and *Brachypodium pinnatum* she also analyzed patches dominated by *Senecio macrophyllus*. She found the highest seed bank density in *Senecio macrophyllus* patch and less in *Brachypodium pinnatum* grassland. She defined longevity categories based on the relation between seed rain and seed bank, viability of seeds, presence in deeper soil layers and stability in soil: (i)species having persistent seed bank, seed rain exceeding the seed bank in soil, seeds detectable in deeper soil layer and permanent presence of diaspores in the soil; (ii)species having high productivity and transient seed bank, seed rain exceeding the seed bank in soil, seeds present in the soil for a short period of time, germinating after shedding, presence in higher number in the upper soil layer and low number in deeper soil layers. The first category was formed by *Carex flacca, C. transsilvanica, Linum flavum, Scabiosa ochroleuca* and *Origanum vulgare,* while the second category included *Aster amellus* and *Senecio macrophyllus.* Czarnecka also found higher species number and seed density in the shaded patches of *Senecio macrophyllus* grassland in the vicinity of a *Rhamno-Prunetea* brushwood than in *Brachypodium pinnatum* dominated unshaded patches. She concluded that under adult plants and in small hollows the special microhabitats prevented the water shortage and offered lower temperature than open places. She observed a nurse effect, i.e., the special microhabitat created by the adult plant which provided more adequate circumstances for seed and seedling survivorship which can lead to a higher seed density and species richness in shaded patches. In another papers (Czarnecka 2005, 2008) she compared the seed banks of xerothermic grasslands, brushwoods and woodlands. The highest seed diversity was present in grassland (Table 1) and the lowest in woodland, the highest seed density in brushwood and lowest in woodland. The seed bank of brushwood and grassland were similar because of the presence of the similar herb layer. With the bush encroachment the seed bank of grassland species decreased and the number of brushwood and woodland species increased. In brushwood the share of endozoochores also increased and the seed density of former dominant *Origanum vulgare* decreased.

### *3.4.2. Mountain Grasslands*

#### 3.4.2.1. Subalpine Grasslands

One paper studied seed banks changes along primary succession on a glacier foreland in the Central Alps (Marcante et al. 2009). The initial stage of primary succession was considered a site which was ice-free since 33 years. The second and third stages were deglacied from 81 and 146 years respectively, and old succession stage was considered a subalpine pasture ice-free more than 5000 years. In this study a continuous increase of seed bank density was found during succession. In the pioneer stage the seed bank density was the highest in 2-5 cm depth. The total seed density increased in upper soil layers in course of succession. Seed banks of subalpine pastures also contained many seeds in deeper soil layer. Morisita-Horn similarity was high between aboveground vegetation and seed bank of upper soil layers (37-61), but there was a decreased similarity with increasing age and in the subalpine pasture the composition of aboveground vegetation was more similar to that of the seed bank in the deeper soil layer (63).

### 3.4.2.2. Dry Calcareous Grasslands

Karlík and Poschlod (2014) studied the seed banks of ancient grasslands and old-fields with secondary dry calcareous grassland vegetation in two regions of Germany (Kallmünz, a lower-elevated and Kaltes Feld, a higher-elevated sites with grasslands of *Gentiano-Koelerietum* association). In Kallmünz region vegetation was characterised by higher number of xerothermic species, which were rather rare in the vegetation in Kaltes Feld). Both regions harboured recently abandoned arable fields and old-fields with secondary grassland vegetation. In the lower elevated region of Kaltes Feld only a sparse seed bank of typical dry grassland species were found and these species were present only in the seed banks of ancient grasslands. In old-fields several arable weed species and typical fallow field species were frequent. Grasslands in the lower-elevated xerothermic region were more species-rich while the other region was characterized by higher seed density. They found the lowest species richness in the recently abandoned arable fields and in the ancient grasslands and concluded that there is no linear relationship between the age of grassland and species number of seed banks in both sites. Contrary, seed bank density showed an opposite trend, decreasing in the lower elevated region and increasing in the higher elevated region with the field age. Ancient grasslands had the highest proportion of typical dry grassland species while old-fields had the highest proportion of mesophylous grassland species and weedy species. Surprisingly, some seeds of rare and endangered species (*Kickxia spuria, Neslia paniculata, Phleum nodosum, Silene noctiflora, Stachys annua*) were present in the seed bank of old-fields in both regions.

We found one other study on calcareous grasslands (Klimešová et al. 2013) from the Czech Republic. The aim of the study was to analyze if there is a negative correlation between the traits relevant for competitive ability of species and their generative regeneration. Species with high competitive ability were characterized with erosulate shoots, good lateral spreading ability and large seeds. Species which relied on generative regeneration were characterized by low stature, easy-dispersed seeds and ability to form a dense seed bank. Researchers concluded that the latter group disappeared first from vegetation after abandonment of semi-natural grasslands but they also have the potential to recolonize the sites from seed bank after management is re-introduced. They found a competitive colonization trade-off, because the studied plant traits relevant for competitive ability and generative regeneration correlated negatively. Species which preferred clonal growth had larger seeds in a smaller number while species without clonal growth had high number of small seeds.

### 3.4.2.3. Mesic Grasslands

Seed banks of mesic grasslands in Germany were studied by Wellstein et al. (2007). They found the dominance of a few species (*Trifolium repens*, *Agrostis capillaris*, *Plantago lanceolata*, *Juncus bufonius*, *Leontodon autumnalis*, *Poa trivialis* and *Cerastium holosteoides*) in the seed bank. Species with high seed accumulation capacity and mostly persistent seeds were rare or absent from vegetation.


Figure 5. Mesic grasslands in Mátra, Northeast Hungary. Photos of András Kelemen.

Species of disturbed habitats and some grassland species had the highest seed accumulation index (SAI, combining two indices which express the relation between the presence of certain species in vegetation and soil seed bank, Hölzel and Otte 2004). The species with the lowest seed accumulation capacity were grassland species. The seed banks of pastures were characterized mainly by ruderal species such as *Plantago major* and *Urtica dioica.* Silage meadows were indicated by arable weeds like *Capsella bursa-pastoris.* Meadows (the studied hay meadows and silage meadows) and meadow-pastures (late mowing and subsequent grazing) contained species characteristic of nutritient-poor conditions, such as *Luzula campestris* and *Potentilla erecta.* The last two are considered to be stress-tolerant species similar to *Pimpinella saxifraga, Carex ovalis* and *Veronica chamaedrys.* Stress-tolerant species were typical in the seed banks of meadows and meadow-pastures, while competitors like *Dactylis glomerata* were evenly distributed among grasslands with different management types. Ruderals contributed with nearly a half of total density to the seed banks of grasslands regardless to the management type (Figure 5).

#### 3.4.2.4. *Festuco-Brometea* and *Arrhenatheretalia*-Type Grasslands

Zeiter et al. (2014) studied the relation between seed bank and community productivity. The study was conducted in temperate semi-natural grasslands in Switzerland which were extensively used for hay making. Pairs of extensively and intensively mown sites were analyzed. They found correlation between seed density and species richness of topsoil seed bank and the seed rain. The seed bank density correlated positively with community productivity, but the species richness showed only marginal significant correlation with productivity. The proportion of annual and perennial forb species with persistent seed bank and the persistent seed bank density correlated negatively with community productivity.

#### 3.4.2.5. Dry-Mesophylous Grasslands with *Brachypodium pinnatum*

This type of meadow was studied in Hungary by Valkó et al. (2011). The results showed similar species richness to fen meadows but a lower seed density. Fewer species of vegetation formed seed bank (26%) and according to this the similarity between seed bank and aboveground vegetation was also lower than found in fen meadows (0.28-0.36). Few species formed persistent seed bank (33% of all species). Protected species were missing from seed bank. Common rushes like *Juncus conglomeratus* and *J. effusus* were only present in the seed bank (Figure 6).

Figure 6. Mountain hay meadows in Zemplén Mountains, Northeast Hungary. Photos of Tamás Miglécz.

### 3.4.2.6. Other Grassland Types

Handlová and Münzbergová (2006) studied managed and abandoned mountain grasslands in the Czech Republic. They found that the seed bank and vegetation had similar species richness but there was difference in their species composition. Typical species of the vegetation generally had only sparse seed banks. There were also differences in the species composition of degradation stages. The similarity between seed bank and aboveground vegetation was also low. Degraded plots had more species in their seed bank than in the aboveground vegetation. In non-degraded plots the opposite was true. Close patches showed higher dissimilarity than remote patches. The degradation increased the heterogenity of seed banks.

### *3.4.3. Wet Grassland Types*

#### 3.4.3.1. Fen Meadows

Valkó et al. (2011) studied mown and abandoned dry-mesophilous meadows and acidic fen meadows in Hungary. They found that managment type had only effect on the seed bank composition of fen meadows. *Molinia arundinacea* had higher seed density in abandoned plots while *Agrostis canina* and *Lychnis flos-cuculi* in mown plots. The species richness of fen meadows was similar to that of dry-mesophilous meadows but a higher seed density was detected and also more herb species were typical in the seed banks of fen meadows. In fen meadows 44% of species from vegetation had a seed bank and accordingly the similarity between seed bank and vegetation reached values of 0.41-0.53. 49% of species were persistent, almost all frequent graminoids of vegetation had considerable seed bank. Common rushes (especially *Juncus conglomeratus* and *J. effusus*) were present only in seed bank and the study also revealed that many protected species lacked persistent seed banks.

The seed bank of fens along a degradation gradient was studied in Germany and Poland by Klimkowska et al. (2010). The results showed a decrease in seed bank density, diversity and an increase of the number of persistent species with increasing level of degradation. The number of species with perennial bud bank also decreased with increasing level of degradation. In the first stage of degradation (i.e., the transformation of fens to fen meadows), the number of species with perennial bud bank decreased in the seed bank and species number with shorter life span and persistent seed bank increased. In the second stage (i.e., transformation of fen meadows to degraded fen meadows) the number of species with a long flowering period and long-term persistent seed bank increased.

#### 3.4.3.2. Alluvial Meadows

Seed banks in floodplains with different management and topography were analyzed by Havrdová et al. (2015). The results showed that seed density and species diversity was higher in the upper soil layer but most species were present both in the upper and deeper soil layers. The species found only in the upper soil layer had transient seed banks but species found in deeper soil layers were probably persistent. The seed bank was dominated by only few species (*Juncus* spp., *Hypericum maculatum, Agrostis capillaris*). The topography and management together had a major effect on seed bank composition. The low elevated plots ungrazed less than 40 years had the highest seed density while plots of high elevation ungrazed for more than 40 years had the lowest seed density. Low topography in case of every management type resulted higher seed density compared to high elevation even though results were not significant. Franczak and Czarnecka (2015) studied the effect of waterlogging on the seed bank of moist floodplain meadows with *Lysimachio vulgaris-Filipenduletum* association. They found that prolonged waterlogging had major effects on vegetation but did not induce major changes in seed bank. The species diversity and richness decreased both in the waterlogged and control patches but it was not significant. After the withdrawal of waterlogging in the waterlogged patch the seed bank density was slightly higher than in the initial stage. In the control patch, which was not affected by waterlogging, the seed density decreased, but not significantly. In both patches the share of meadow species increased. The seed bank was dominated by three species (*Carex acutiformis*, *Lysimachia vulgaris* and *Lythrum salicaria*). The similarity between the species composition of seed banks and aboveground vegetation decreased in the waterlogged patch, increased in the control patch.

#### 3.4.3.3. *Cirsietum rivularis* Meadow

Falińska (1998, 1999) analyzed the seed banks of former meadows during succession for 20 years in Poland. The vegetation and the seed bank of the studied sites were monitored beginning from 1976 in every five years at the beginning and the end of the growing season. The seed bank density was low in the first stage after abandonment, then increased for 5-15 years and declined again thereafter. Almost all species from the vegetation contributed to the seed bank. The changes detected in the seed bank were slower than in the vegetation, grassland species were also present in the seed bank of young forests. She also noticed the decrease of meadow species seed bank and the increase of forest species during succession.

#### 3.4.3.4. *Caricion davallianae* Meadow

Bekker at al. (1997) analyzed the seed banks of wet meadows in Germany which were subjected to hydrological changes and cessation of management. The results showed major impact of geography, climate and landscape effects in the seed bank of all studied grasslands. Seed banks of the same country were more similar to each other than to other countries seed bank. In Germany species indicating mid-ranged nutritient conditions reached the highest proportion in the reference sites upper soil layer. In the deeper soil layer mainly indicators of poor nutritient conditions were present alongside with indicators of rich-nutritient conditions.

#### 3.4.3.5. Oligothrophic Wet Meadows

Weiterová (2008) studied oligothrophic wet meadows in the Czech Republic. She found the highest seed numbers in spring samples and noted that all species from seed bank were also present in vegetation. Sedges were the most common species in the seed banks, while grasses were only poorly represented. Sedges also dominated gaps seed bank and penetrated more easily in deeper soil layers than other species.

#### 3.4.3.6. *Deschampsia cespitosa* Dominated Grasslands

Matějková et al. (2003) found large differences between the seed bank and aboveground vegetation composition in mountain grasslands in the Czech Republic. The study site was a species-poor sward dominated by *Deschampsia cespitosa* in a semi-natural pasture. The grazingwas re-introduced in 1995. The seed bank of the studied plots contained seed of typical species of *Deschampsia caespitosa* community. Few species typical of species-rich grasslands (*Alchemilla monticola, Carex panicea, Juncus filiformis, Luzula multiflora, Veronica officinalis*) contributed to the seed bank which was formed mainly by seeds of ruderal species and weedy species of wet habitats like *Urtica dioica, Juncus bufonius, J. effusus* and *Sagina procumbens*. In the cattle dung they found species which were not present in vegetation, mainly common grasses, sedges and ruderal dicots. They concluded that grazing alone is not an effective tool for the restoration of species-rich grasslands. Combining grazing with regeneration from seed bank is still ineffective because seed banks also missed these characteristic species and had an increasing proportion of pioneers and ruderals. Cattle dung was inadequate for seed dispersal because species-rich patches were poorly grazed and digestion also may damage seeds.

### *3.4.4. Other Grassland Types*

#### 3.4.4.1. Grasslands on Degraded Debris Disposal, Industrial Contamination and Urban Wastelands

Stroh et al. (2002) studied former debris disposal areas in Germany to find out if grazing is an effective tool for sand grassland restoration. They found that the seed bank of the studied area was poor in species and was dominated by ruderal species. The similarity between the seed bank of debris disposal areas and that of target sand grasslands was very low. Grazing itself was not an effective way for restoration but combined with diaspore adding methods it was feasible for the restoration of target vegetation.

In industrial contamined site three years of succession was studied (Wagner et al. 2006). The results showed an increase in seed number in the upper soil layer over time. In contrast the total seed density has not changed. The density of colonizer species increased. The most abundant species in the seed bank was *Puccinellia distans* despite that it was not present in the vegetation. Four other species also had high share in soil seed bank (*Cerastium glutinosum, Epilobium tetragonum, Chenopodium rubrum, Atriplex sagittata*). In the third stage of succession the upper soil layers seed bank showed high similarity with aboveground vegetation but the deeper soil layers remained more similar to the former vegetation.

In grasslands formed on urban wastelands (Albrecht et al. 2011) the soil seed density showed positive correlation with the vascular plant cover and the seed density produced by vegetation but it was not correlated with moss cover. The dissimilarity between the seed bank composition and aboveground vegetation was high. Contrary to most of the studies, the seed bank was dominated by biennial and perennial ruderal species, the share of annuals was low. The species were mostly species of open sandy and rocky outcrops, alien species and oligothrophic and productive grassland species. The species composition of the upper and lower soil layers was similar. The seed bank contained seeds of ten species from the Red Book of Germany and Bavaria, such as *Centaurea stoebe*, *Medicago minima*, *Minuartia hybrida* and *Teucrium botrys*. They also noticed that species from the summer seed rain had shorter longevity than species from the early spring seed bank.

### 3.4.4.2. Secondary Grasslands

Studies on the seed banks of former arable fields (Dölle and Schmidt 2009, Török et al. 2012) noticed the positive effect of disturbance on the soil seed density and also the negative effect of age on seed bank richness (Dölle and Schmidt 2009). Dölle and Schmidt (2009) also showed that disturbances increased the seed density on deeper soil layers compared to undisturbed sites. The similarity between the species composition of soil seed banks and aboveground vegetation was also higher in disturbed sites.The invasive goldenrod species, *Solidago canadensis* was widely distributed and dominated the seed bank but other species also appeared to be widespread with high seed density (*Arenaria serpyllifolia*, *Betula pendula* and *Chaenorrhinum minus*). Arable field species were able to accumulate high seed density in contrast woody species had no or only sparse seed bank. The R strategists had higher share in the seed bank than in the aboveground vegetation and C strategists had the highest share in infrequently mown plots. Török et al. (2012) found that weedy and fallow species were typical in the seed banks of regressed former arable fields in Hungary. *Capsella bursa-pastoris* was the most widespread seed bank species reaching the highest abundances in former alfalfa fields. *Echinochloa crus-galli* preferred former cereal and sunflower fields, *Gypsophila muralis* and *Matricaria chamomilla* had high densities in former alfalfa and cereal fields which were restored with alkali seed mixtures.

In a succession study Kwiatkowska-Falińska et al. (2011) studied former meadows and fresh coniferous forests developed in meadows. They found that during the succession *Calluna vulgaris* became dominant in the seed bank of fallows but its seed density decreased significantly in the forest seed bank. The annual-biennial segetal and fallow species and psammophilous species were present in seed bank with a higher number in the beginning of succession which decreased during succession. Persistent seeds apear in the seed bank after 16 years because of the presence of bryophytes and lichens which made harder for diaspores to reach the soil layer. The share of persistent seeds increased continuously. They also calculated longevity index of species, which increased over the succession phases. In the last stage of succession trees caused the decline of heliophilous species and also bryophytes and lichenes disappeared which resulted in the diversification and accumulation of seeds with different longevity in the seed bank. In the course of succession similarity between seed bank and aboveground vegetation increased in the first stages of succession and decreased thereafter. From the vegetation species disappeared faster than from the seed bank where the seed density of species decreased only gradually.

## 4.General Conclusion

### 4.1.Seed Size and Other Plant Traits

In some studies the changes of different seed features in seed bank were also monitored. Weiterová (2008) noticed the change of the proportion of light/heavy seeds during the vegetation period and found more light seeds in spring samples. Hay meadows are characterized by the highest mean specific seed mass and cattle pastures by the lowest ones. Pastures are more disturbed habitats where the establishment in gaps is favoured in contrast with more stable meadow habitats where competition favours large-seeds (Wellstein et al. 2007). Zeiter et al. (2014) observed a decrease of seed size with increasing productivity which was in contrast with their expectations. They explained this contradiction with the opposite selective forces for seed size of increasing productivity and disturbance. The share of endozoochorous seeds increased through succession from grassland to forest (Czarneczka 2008), in forest seed bank mainly endozoochorous, anemochorous and myrmecochorous species were present (Czarnecka 2005).

The most typical life form in urban wastelands of species found only in seed bank were hemicryptophytes, mainly biennials, followed by therophytes and only one species was geophyte (Albrecht et al. 2011). In the study of Karlík and Poshold (2014) the result showed that young grasslands hosted higher number of therophytes but their number decreased with age and in ancient grasslands hemicryptophytes dominated. Chamaephytes were present only in small number in ancient fields.

Koch et al. (2011) also observed the hemicryptophytes being the most represented life form in seed banks. Klimešová et al. (2013) found that rosette and semirosette species had numerous small seeds and a high seed accumulation index while taller species preferred clonal growing or have only a small number of seeds. Karlík and Poshold (2014) also noticed on average more elongate seeds in the seed banks of ancient grasslands. Their findings are in accordance with other studies. Ancient grasslands are quite stable habitats and therefore grassland species invest in the seedling establishment and competitive ability more than in surviving of unfavourable conditions (Bossuyt and Honnay 2008).

Typical grassland species have transient or short-lived seeds (Thompson et al. 1997) which is often associated with seed morphology, like seed mass and shape. Transient or short-term persistent seeds are flattened and elongated while long-term persistent seeds are small and have spherical shape (Thompson et al. 1993, Schwienbacher et al. 2010).

## 4.2.Environmental Factors and Seed Bank Composition

Several studies of different grassland types revealed a significant effect of topography on seed bank density and diversity. Czarnecka (2004a) found similar avarage seed number in the two studied elevations but different composition despite the fact that some species were common in both elevations. Török et al. (2009) found higher seed density in seed bank in higher elevated sites and with this the similarity with the aboveground vegetation species composition it was also higher. Similar results were published earlier by Matus at al. (2003). Another study from Hungary found a significant effect of elevation on seed bank in alkali grasslands (Valkó et al. 2014). With the elevation other environmental parameters also changed so the soil water capacity, organic matter and soil water content was the highest in the lower elevation and the salinity the lowest. They found that the elevation was the only environmental factor which had a significant effect on the seed density and diversity. In this study the highest seed density and seed bank diversity was found at the lowest elevation. In the fields studied by Havrdová et al. (2015) the seed bank reached the highest density in lower elevations in the grassland unmanaged for less than 40 years, likely because decreased light intensity at the soil surface, which was considered as decisive for seed germination (Kettenring et al. 2006). Seed accumulation could also increase because plants were not mown before the seed maturisation. Depletion after 40 years may be caused by natural loss of seed viability, seed degradation by pathogens and seed predation. In yearly mown sites the seed bank density was higher in lower elevations. The similarity between species composition of seed banks and aboveground vegetation was also higher in low elevation. Based on these findings they supposed that the predictability of seed bank from vegetation was possible especially in low elevations. Besides elevation Albrecht et al. (2011) found positive correlation between the seed number of soil seed bank and the concentration of mineralized nitrogen and phosphorous. The correlation with the percentage of calcareous gravel>2 mm and to pH was negative.

## 4.3.The Role of Seed Banks in Grassland Restoration

Seed banks represent an important propagule source, but the extent that we can rely on regeneration from local seed banks depend on many factors, such as site history, landscape composition, degradation status and grassland type. Despite the fact that most research confirmed that typical species disappear at the long-term from the persistent seed bank after the cessation of grassland management restoration could be possible on the short-run. This assumption was supported by the findings of Matus et al. (2003) and Valkó et al. (2011). Matus et al. (2003) studied the seed bank of sand grasslands released from grazing and now abandoned. They found that sensitive species disappeared already in the first stages of succession while typical species of sand grasslands were still present in the seed bank so the restoration was still possible. Valkó et al. (2011) studied fen meadows and dry-mesophylous grasslands. In fen meadows they found enough seeds in the seed bank for partial recovery. In contrast dry-mesophillous grasslands had a poor seed bank, in this case not even partial restoration was possible. They also stated that re-introducing mowing regimes can be an effective tool of restoration in fen meadows.

Few studies found a lower seed density and species diversity in the first decades after abandonment compared to later stages in semi-natural grasslands (Falińska 1998, 1999, Havrdová et al. 2015) which increased with time. The increase may be due to the possibility of plants to flower and produce seeds and also due to lack of litter and bryophyte layer which prevent seeds from entering the soil. The best practice for successful restoration by spontaneous succession may be the reintroduction of management in this temporary stage before seed trapping and seed degradation occur. Besides this human intervention can be avoided if surrounding areas are in good condition and contains target species (Ruprecht 2006, Török et al. 2010).

In many cases vegetation recovery from the seed bank is not possible without human intervention. Contrary to previous studies Matus et al. (2003) noticed the decreasing seed density and diversity with time from cattle grazing release. Species with transient or short-term persistent seeds disappeared from seed bank disabling the use of seed bank for restoration purposes. Some patches were invaded by *Robinia pseudo-acacia* and contained only few grassland species and several pioneer weedy species. These species after the removing of *Robinia* stands may lead to the formation of species-poor weedy pastures not the original sand grasslands. Matějková et al. (2003) also states that seed bank has little effect on grassland restoration because of the lack of typical grassland species and a high proportion of pioneers and ruderal species. They also analyzed cattle dung as a source of propagules but it lacked typical grassland species and seeds were also damaged during digestion so cattle dung was ineffective in propagule dispersion. Stroh et al. (2002) studied spontaneous succession and restoration with diaspore addition and grazing. They found that patches which received diaspores and were grazed in the same time revegetated faster than the unmanaged or only grazed patches and became biodiversity hotspots. Seed bank alone had minor role in the restoration. Other studies of different grassland types also stated that seed bank alone is not enough for restoration, the transient nature of species lead to a limited species and seed number. Bossuyt et al. (2006) found only sparse calcareous grassland seed bank in a deforested study site in Belgium.

Jacquemin et al. (2011) also stated that seed bank is not enought to restore abandoned calcareous grassland because of the disappearance of typical species. The same was found by Metsoja et al. (2014) in flooded meadows, i.e., that seed banks alone are not enough for restoring species-rich grasslands. If the seed bank is still present but contains only a low density of seeds and the species richness is also low then human intervention can help restoration processes. Traditional mowing or grazing are used in restored or semi-natural grasslands to increase or maintain species richness (Jacquemin et al. 2011, Koch et al. 2011, Török et al. 2014). Grazing and mowing can accelerate restoration processes by preventing litter accumulation which can work as a seed trap (Kelemen et al. 2014, Ruprecht and Szabó 2012) and by removing the present litter which open new gaps for further colonization. Grazing is also a tool for propagule introduction (Matus et al. 2005, Tölgyesi et al. 2015, Tóth et al. 2016, Matějková et al. 2003), which is not true in the case of mowing.

If degradation level is too high and seed bank contains only a relatively low proportion of target species or when seed bank is missing, neighbouring site is fragmented and there are no suitable seed sources than the restoration depends on the artificial introduction of species. This is possible in different ways: sowing of seed mixtures, plant material transfer, topsoil transfer, turf transplantation, community translocation (Török et al. 2011, Valkó et al. 2016c). For sowing low-diversity seed mixtures or high-diversity seed mixtures are used. This method was used by Török et al. (2012). The studies conducted in restored sites showed that after three years of sowing short-lived weed species were missing from the vegetation but they were still present in soil seed banks with a high density.

## ACKNOWLEDGMENTS

OV was supported by OTKA PD 111807, PT by NKFIH K 119225 and BT by OTKA K 116639 projects. The publication was supported by the SROP-4.2.2.B-15/1/KONV-2015-0001 project supported by the European Union, co-financed by the European Social Fund. OV was supported by the János Bolyai Research Scholarship of the Hungarian Academy Sciences and the NTP-NFTÖ-16-0107 project by the Human Capacities Grant Management Office and the Hungarian Ministry of Human Capacities. RK was supported by the scholarship of Ministry of Human Resources and the Balassi Institute.

## REFERENCES


Albrecht, H., Eder, E., Langbehn, T. and Tschiersch, C. (2011). The soil seed bank and its relationship to the established vegetation in urban wastelands. *Landscape and Urban Planning, 100,* 87-97.

Bekker, R. M., Verweij, G. L., Smith, R. E. N., Reine, R., Bakker, J. P. and Schneider, S. (1997). Soil seed banks in European grasslands: Does land use affect regeneration perspectives? *Journal ofApplied Ecology, 34,* 1293-1310.

Blomqvist, M. M., Bekker, R. M. and Vos, P. (2003). Restoration of ditch bank plant species richness: The potential of the soil seed bank. *Applied Vegetation Science, 6,* 179-188.

Bossuyt, B., Butaye, J. and Honnay, O. (2006). Seed bank composition of open and overgrown calcareous grassland soils-a case study from Southern Belgium. *Journal of Environmental Management, 79,* 364-371.

Bossuyt, B. and Honnay, O. (2008). Can the seed bank be used for ecological restoration? An overview of seed bank characteristics in European communities. *Journal of Vegetation Science, 19,* 875-884.

Chytrý, M., Dražil, T., Hájek, M., Kalníková, V., Preislerová, Z., Šibík, J., Ujházy, K., Axmanová, i., Bernátová, D., Blanár, D., Dančák, M., Dřevojan, P., Fajmon, K., Galvánek, D., Hájková, P., Herben, T., Hrivnák, R., Janeček, S., Janišová, M., Jiráská, S., Kliment, J., Kochjarová, J., Lepš, J., Leskovjanská, A., Merunková, K., Mládek, J., Slezák, M., Šeffer, J., Šefferová, V., Škodová, I., Uhlířová, J., Ujházyová, M. and Vymazalová, M. (2015). The most species-rich plant communities in the Czech Republic and Slovakia (with new world records). *Preslia, 87*, 217-278.

Czarnecka, J (2004a). Microspatial structure of the seed bank of xerothermic grassland-intracommunity differentiation. *Acta Societatis Botanicorum Poloniae, 73*, 155-164.

Czarnecka, J (2004b). Seed longevity and recruitment of seedlings in xerothermic grassland. *Polish Journal of Ecology, 52*, 505-521.

Czarnecka, J (2005). Seed dispersal effectiveness in three adjacent plant communities: xerothermic grassland, brushwood and woodland. *Annales Botanici Fennici, 42*, 161-171.

Czarnecka, J (2008). Spatial and temporal variability of seed bank resulting from overgrowing of xerothermic grassland. *Acta Societatis Botanicorum Poloniae, 77,* 157-166.

Deák, B., Hüse, B. and Tóthmérész, B. (2016). Grassland vegetation in urban habitats – testing ecological theories. *Tuexenia, 36,* 379-393.

Dengler, J., Janišová, M., Török, P. and Wellstein, C. (2014). Biodiversity of paleaearctic grasslands: a synthesis. *Agriculture, Ecosystems and Environment, 182,* 1-14.

Dölle, M. and Schmidt, W. (2009). The relationship between soil seed bank, above-ground and disturbance intensity on old-field successional permanent plots. *Applied Vegetation Science, 12*, 415-428.

Falińska, K. (1998). Long-term changes in size and composition of seed bank during succession: from meadow to forest. *Acta Societatis Botanicorum Poloniae, 67,* 301-311.

Falińska, K. (1999). Seed bank dynamics in abandoned meadows during a 20-year period in the Białowieża National Park. *Journal of Ecology, 87,* 461-475.

Franczak, M. and Czarnecka, B. (2015). Changes in vegetation and soil seed bank of meadow after waterlogging caused by *Castor fiber. Acta Societatis Botanicorum Poloniae, 84,* 189-196.

Handlová, V. and Münzbergová, Z. (2006). Seed banks of managed and degraded grasslands in the Krkonoše Mts., Czech Republic. *Folia Geobotanica, 41*, 275-288.

Havrdová, A., Douda, J. and Doudová, J. (2015). Local topography affects seed bank successional patterns in alluvial meadows. *Flora, 217,* 155-163.

Hölzel, N. and Otte, A. (2004). Assessing soil seed bank persist- ence in flood-meadows: The search for reliable traits. *Journal of Vegetation Science,15*, 93-100.

Hong, J., Liu, S., Shi, G. and Zhang, Y. (2012). Soil seed bank techniques for restoring wetland vegetation diversity in Yeyahu Wetland, Beijing. *Ecological Engineering, 42,*192-202.

Hopfensperger, K. N. (2007). A review of similarity between seed bank and standing vegetation across ecosystems. *Oikos, 116,* 1438-1448.

Jacquemyn, H., VanMechelen, C., Brys, R.& Honnay, O. (2011). Management effects on the vegetation and soil seed bank of calcareous grasslands: An 11-year experiment. *Biological Conservation, 144*, 416-422.

Karlík, P. and Poschlod, P. (2014). Soil seed-bank composition reveals the land-use history of calcareous grasslands. *Acta Oecologica, 58*, 22-34.

Kelemen, A., Török, P., Valkó, O., Deák, B., Miglécz, T., Tóth, K., Ölvedi, T. and Tóthmérész, B. (2014). Sustaining recovered grasslands is not likely without proper management: vegetation changes and large-scale evidences after cessation of mowing. *Biodiversity and Conservation, 23,* 741-751.

Kemény, G., Nagy, Z.& Tuba, Z. (2005). Seed bank dynamics in a semiarid sandy grassland in Hungary. *Ekológia (Bratislava), 24*, 1-13.

Kettenring, K. M., Gardner, G. and Galatowitsch, S. M. (2006). Effect of Light on Seed Germination of Eight WetlandCarexSpecies. *Annals of Botany, 98,* 869-874.

Klimešová, J., Mudrák, O., Doležal, J., Hájek, M., Dančák, M. and Klimeš, L. (2013). Functional traits in a species-rich grassland and a short-term change in management: is there a competition-colonization trade-off? *Folia Geobotanica, 48*, 373-391.

Klimkowska, A., Bekker, R. M., van Diggelen, R. and Kotowski, W. (2010). Species trait shifts in vegetation and soil seed bank during fen degradation. *Plant Ecology, 206,* 59-82.

Koch, M. A., Scheriau, C., Schupfner, M. and Bernhardt, K.-G. (2011). Long-term monitoring of the restoration and development of limestone grasslands in north western Germany: Vegetation screening and soil seed bank analysis. *Flora, 206*, 52-65.

Koncz, G., Török, P., Papp, M., Matus, G. and Tóthmérész, B. (2011). Penetration of weeds into the herbaceous understorey and soil seed bank of a Turkey oak-sessile oak forest in Hungary. *Community Ecology, 12*, 227-233.

Kwiatkowska-Falińska, A. J., Jankowska-Błaszczuk, M. and Wódkiewicz, M. (2011). The pattern of seed banks during secondary succession on poor soils. *Acta Societatis Botanicorum Poloniae, 80*, 269-274.

Marcante, S., Schwienbacher, E. and Erschbamer, B. (2009). Genesis of a soil seed bank on a primary succession in the Central Alps (Ötztal, Austria). *Flora, 204*, 434-444.

Matějková, I., van Diggelen, R. and Prach, K. (2003). An attempt to restore a Central European species-rich mountain grassland through grazing. *Applied Vegetation Science, 6,* 161-168.

Matus, G., Tóthmérész, B. and Papp, M. (2003). Restoration prospects of abandoned species-rich sandy grassland in Hungary. *Applied Vegetation Science, 6*, 169-178.

Matus, G., Tóthmérész, B. and Papp M. (2005). Impact of management on vegetation dynamics and seed bank formation of inland dune grassland in Hungary. *Flora, 200,*296-306.

McDonald, A. W. (1993). The role of seedbank and sown seeds in the restoration of an English flood-meadow. *Journal of Vegetation Science, 4,* 395-400.

Metsoja, J.-A., Neuenkamp, L. and Zobel, M. (2014). Seed bank and its restoration potential in Estonian flooded meadows. *Applied Vegetation Science, 17*, 262-273.

Plassmann, K., Brown, N. Jones, M. L. and Edwards-Jones, G. (2009). Can soil seed banks contribute to the restoration of dune slacks under conservation management? *Applied Vegetation Science, 12,* 199-210.

Rosef, L. (2008). Germinable soil seed banks in abandoned grasslands in central and western Norway and their significance for restoration. *Applied Vegetation Science, 11,* 223-230.

Ruprecht, E. (2006). Successfully Recovered Grassland: A Promising Example from Romanian Old-Fields. *Restoration Ecology, 14,* 473-480.

Ruprecht, E. and Szabó, A. (2012). Grass litter is a natural seed trap in long-term undisturbed grassland. *Journal of Vegetation Science, 23,* 495-504.

Schwienbacher, E., Marcante, S.& Erschbamer, B. (2010). Alpine species seed longevity in the soil in relation to seed size and shape – A 5-year burial experiment in the Central Alps. *Flora, 205*, 19-25.

Stroh, M., Storm, C., Zehm, A. and Schwabe, A. (2002). Restorative grazing as a tool for directed succession with diaspore inoculation: the model of sand ecosystems. *Phytocoenologia, 32,* 595-625.

Stroh, P. A., Hughes, F. M. R., Spars, T. H. and Mountford, J. O. (2012). The influence of time on the soil seed bank and vegetation across a landscape-scale wetland restoration project. *Restoration Ecology, 20*, 103-112.

Thompson, K., Bond, R. S. and Hodgons, J. G. (1993). Seed size and shape predict persistence in soil. *Functional Ecology, 7,* 236-241.

Thompson, K., Bakker, J. P. and Bekker, R. M. (1997). *The soil seed banks of North West Europe: Methodology, density and longevity.* Cambridge, Cambridge University Press.

Tóth, E., Deák, B., Valkó, O., Kelemen, A., Miglécz, T., Tóthmérész, B. and Török, P. (2016). Livestock type is more crucial than grazing intensity: Traditional cattle and sheep grazing in short-grass steppes. *Land Degradation and Development,* doi:10.1002/ldr.2514.

Tóth, K. and Hüse, B. (2014). Soil seed banks in loess grasslands and their role in grassland recovery. *Applied Ecology and Environmental Research, 12*, 537-547.

Tölgyesi, C., Bátori, Z., Erdős, L., Gallé, R. and Körmöczi, L. (2015). Plant diversity patterns of a Hungarian steppe-wetland mosaic in relation to grazing regime and land use history. *Tuexenia, 35*, 399-416.

Török, P., Matus, G., Papp, M. and Tóthmérész, B. (2009). Seed bank and vegetation development of sandy grasslands after goose breeding. *Folia Geobotanica, 44*, 31-46.

Török, P., Kelemen, A., Valkó, O., Deák, B., Lukács, B. and Tóthmérész, B. (2010). Lucerne-dominated fields recover native grass diversity without intensive management actions. *Journal of Applied Ecology, 48,* 257-264.

Török, P., Vida, E., Deák, B., Lengyel, Sz. and Tóthmérész, B. (2011). Grassland restoration on former croplands in Europe: An assessment of applicability of techniques and costs. *Biodiversity and Conservation, 20*, 2311-2332.

Török, P., Deák, B., Valkó, O., Kelemen, A., Kapocsi, I., Miglécz, T. and Tóthmérész,B. (2012). Recovery of alkaline grassland using native seed mixtures in the Hortobágy National Park (Hungary). In K. Kiehl, A. Kirmer,Shaw N. and S. Tischew (Eds.), *Guidelines for native seed production and grassland restoration* (pp. 182-197). Cambridge, Cambridge Scholars Publishing.

Török, P., Valkó, O., Deák, B., Kelemen, A. and Tóthmérész, B. (2014). Traditional cattle grazing in a mosaic alkali landscape: Effects on grassland biodiversity along a moisture gradient. *PLoS ONE, 9*, e97095.

Valkó, O., Török, P., Tóthmérész, B. and Matus, G. (2011). Restoration potential in seed banks of acidic fen and dry-mesophilous meadows: Can restoration be based on local seed banks? *Restoration Ecology, 19,* 9-15.

Valkó, O., Török, P., Matus, G. and Tóthmérész, B. (2012). Is regular mowing the most appropriate and cost-effective management maintaining diversity and biomass of target forbs in mountain hay meadows? *Flora, 207,* 303-309.

Valkó, O., Tóthmérész, B., Kelemen, A., Simon, E., Miglécz, T., Lukács, B.A. and Török, P. (2014). Environmental factors driving seed bank diversity in alkali grasslands. *Agriculture, Ecosystems and Environment, 182*, 80-87.

Valkó, O.,Zmihorski, M., Biurrun, I., Loos, J., Labadessa, R. and Venn, S. (2016a). Ecology and Conservation of Steppes and Semi-Natural Grasslands. *Hacquetia, 15*, 5-14.

Valkó, O., Deák, B., Török, P., Kelemen, A., Miglécz, T., Tóth, K. and Tóthmérész, B. (2016b). Abandonment of croplands: problem or chance for grassland restoration? Case studies from Hungary. *Ecosystem Health and Sustainability, 2*, e01208.

Valkó, O., Deák, B., Török, P., Kirmer, A., Tishew, A., Kelemen, A., Tóth, K., Miglécz, T., Radócz, S., Sonkoly, J., Tóth, E., Kiss, R., Kapocsi, I., Tóthmérész, B. (2016c). High-diversity sowing in establishment windows: a promising new tool for enhancing grassland biodiversity. *Tuexenia, 36,* 359-378.

Wagner, M., Heinrich, W. and Jetschke, G. (2006). Seed bank assembly inanunmanaged ruderal grassland recovering from long-term exposure toindustrial emissions. *Acta Oecologica, 30,* 342-352.

Wang, N., Jiao, J.-Y., Jia, Y.-F., Bai, W.-J. and Zhang, Z.-G. (2010) Germinable soil seed banks and the restoration potential of abandoned cropland on the Chinese hilly-gullied loess plateau. *Environmental Management, 46,* 367-377.

Weiterová, I. (2008). Seasonal and spatial variance of seed bank species composition in an oligotrophic wet meadow. *Flora, 203,* 204-214.

Wellstein, C., Otte, A. and Waldhardt, R. (2007). Seed bank diversity in mesic grasslands in relation to vegetation type, management and site conditions. *Journal of Vegetation Science, 18*, 153-162.

Wilson, J. B., Peet, R. K., Dengler, J. and Pärtel, M. (2012). Plant species richness: the world records. *Journal of Vegetation Science, 23*, 796-802.

Zeiter, M., Preukschas, J. and Stampfli, A. (2013). Seed availability in hay meadows: Land-use intensification promotes seed rain but not the persistent seed bank. *Agriculture, Ecosystems and Environment, 171,* 55-62.