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THE ROLE OF SEED BANK AND SEED SOWING IN THE RECOVERY OF GRASSLAND BIODIVERSITY

Egyetemi doktori (PhD) értekezés

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Témavezető

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A doktori értekezés betétlapja

A MAGBANK ÉS A MAGVETÉS SZEREPE GYEPEK DIVÁRZITÁSÁNAK HELYREÁLLÍTÁSÁBAN

THE ROLE OF SEED BANK AND SEED SOWING IN THE RECOVERY OF GRASSLAND BIODIVERSITY

Értekezés a doktori (Ph.D.) fokozat megszerzése érdekében
a Környezettudomány tudományágban
Írta: **Kiss Réka** okleveles Ökológus

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

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Témavezető neve Dr. Deák-Valkó Orsolya

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Introduction

The role of soil seed bank in vegetation dynamics

Seeds are crucial components of the life cycle of vascular plants, securing not only their dispersal and regeneration, but they can also minimize the casualties in case of unfavourable environmental conditions by spreading germination in time and space, enabling also the maintenance of the genetic variability of populations over time (Fenner 1985, Bossuyt & Honnay 2008). The capability of the seeds of some species to restrain germination is the key for survival and long-term persistence. Some seeds cannot germinate either because some of their characteristics inhibit it, so they are in primary or secondary dormancy state (Baskin & Baskin 1998) or the environmental conditions are unfavourable for germination and seeds are in a quiescent state (Baskin & Baskin 1998, Thompson et al. 2003).

Non germinant seeds which enter the soil will form the soil seed bank. According to Csontos (2001) the seed bank is formed by seeds from natural sources, which are independent from their mother plant in their metabolic activities and are able to germinate or will obtain this ability in the future. Many attempts were made to categorize the seeds into seed bank types, including among others seed longevity, germination types and dormancy (Csontos & Tamás 2003). The most commonly used categorization system was presented by Thompson et al. (1997). According to their seed bank classification system, the plant species can be categorized into three main categories depending on how long their seeds can stay viable in soil. The ”transient” category consists of species which have a short-term viability in the soil and they either germinate in one year after ripening or loss viability forever. Many woody and specialist species and also species of undisturbed habitats have transient seeds (Stöcklin & Fischer 1999, Bossuyt & Honnay 2008). Species whose seeds remain viable up to five years form the short-term persistent seed bank. Species who produce seeds which remain viable for more than five years form the long-term persistent seed bank. Persistent seed bank is characteristic to unstable habitats, which suffer from frequent disturbances. Many annuals, short-lived and ruderal species have persistent seeds (Matějková et al. 2003, Wellstein et al. 2007, Török et al. 2009).

The majority of seeds reaching the soil layer remains on the soil surface or in the upper 0-2 (5) cm soil layer, so this upper layer has the highest seed density and species richness (Blomqvist et al. 2003, Bossuyt et al. 2006, Plassmann et al. 2009, Wang et al. 2010). There are special cases, when the deeper soil layers contain more seeds than the upper soil layer. This is called “soil seed bank inversion”, and can occur when due to the soil structure or management practices, like ploughing, seeds can reach the deeper soil layers (Dölle & Schmidt 2003, Marcante et al. 2009, Klimkowska et al. 2010). Generally the movement of seeds in the soil is a slow process; thus, only seeds with a long viability index (persistent seeds) can reach the deeper layers. Bekker et al. (1998a) suggested that the vertical distribution of seeds in the soil correlates with the seed mass and shape. This is in correspondence with other studies (Thompson et al. 1993, Csontos 2010, Schwienbacher et al. 2010, Sonkoly et al. 2014), which found that flattened, elongated and large seeds are generally transient or short-term persistent, while long-term persistent seeds are smaller, have spherical shape, so can move easier in the soil. Exceptions are hard-coated seeds which are generally persistent irrespective of their shape or mass (Csontos 2010). Sonkoly et al. (2014) also found, that species that produce large seeds also produce less seeds in contrast with species which produce a large quantity of small seeds.

The capability of species to produce transient or persistent seeds results in differences between the species composition of the soil seed bank of different habitat types and also between the seed bank and aboveground vegetation. The seed density and species diversity of different habitats can change between large ranges. Bossuyt & Honnay (2008) found, that grasslands and forests have lower seed density than marshes, while species richness and diversity is the highest in case of grasslands. In case of regularly disturbed grasslands similarity between the composition of seed bank and vegetation is generally high (Hopfensperger 2007). We made an overview about seed banks of Central-European grasslands (Kiss et al. 2016), where we found that the lowest species diversity of seed bank can be found in alkaline (Valkó et al. 2014a) and calcareous grasslands (Karlík & Poschlod 2014) of the region, while the highest seed bank diversity was found in loess grasslands (Tóth & Hüse 2014). In case of seed densities primary succession stages are generally characterised by the lowest values (Marcante et al. 2009), and seed density increases towards later successional stages. The lowest seed bank densities were found in case of xerothermic grasslands (Czarnecka 2004) and calcareous sand grasslands (Kemény et al. 2005). The highest seed densities were found in alkaline grasslands (Valkó et al. 2014a) and fen meadows (Valkó et al. 2011).

Transient seeds germinate shortly after dispersal, in autumn or spring in temperate climate or in the first wet season after ripening in other climates(McDonald et al. 1996, Kemény et al. 2005). Thus, their absence from the seed bank is a major reason for the low similarity of vegetation and seed bank, especially in stable habitats where most species have transient seed bank (Bossuyt & Honnay 2008, Kiss et al. 2016). Another cause of the low similarity between vegetation and seed bank may be, that monocot species prefer vegetative spreading and produce only few seeds which also result in their poor presence in the seed bank despite that they can be dominant in the aboveground vegetation (Fenner 1985, Klimešová et al. 2013, Tóth et al. 2015). Finally, some species of primary succession or with low competitive ability are able to stay in the seed bank for a long time. These species are generally displaced in the vegetation but still present in the seed bank (Török et al. 2012, Karlik & Poschlod 2014).

The similarity of vegetation and seed bank is high in grasslands (Hopfensperger 2007, Bossuyt & Honnay 2008) and lower in other habitat types, such as forests or wetlands. In Central European grassland studies the lowest similarity between the seed bank and aboveground vegetation was found in case of former agricultural lands (Török et al. 2009, 2012), while disturbed loess and sandy grassland, alongside with moist meadows had slightly higher similarity (Matus et al. 2005, Tóth & Hüse 2014, Franczak & Czarnecka 2015). Among semi-natural grasslands the similarity was the lowest in case of limestone grasslands (Koch et al. 2011), the highest similarities occurred in case of fen meadows (Valkó et al. 2011) and calcareous grasslands (Karlík & Poschlod 2014). Some studies found, that the average trend is a decreasing similarity between vegetation and seed bank with succession time (Kalamees & Zobel 1998, Török et al. 2012, Hopfensperger 2007) but there are also a few contradicting studies (Karlik &Poschlod 2014).

The timing of sampling and the quantity of soil sampled have major effects on the results of soil seed bank studies. Depending on the purpose of the seed bank study the seed bank sampling can take place in autumn or spring (Csontos 2001). In Europe a sampling in October may give a complete understanding of the seed bank; in this case, samples contain both transient and persistent seeds. Sampling in early spring may lack those transient species which have germinated in autumn (Matus et al. 2005). A late-spring timing of sampling is ideal to focus only on the persistent seed bank, because transient seeds are already germinated, and only the seeds of persistent species remain in the soil (Csontos 2001). The proper sample size is also a crucial factor of seed bank sampling, which varies between habitat types (Csontos 2001). Soil samples need to be taken in similar places with similar abiotic conditions. Small samples can underestimate the composition of the seed bank, but taking too large samples is also problematic, because can overestimate seed bank composition by taking into consideration samples originating from different microclimatic conditions (Bossuyt & Honnay 2008).

For the study of seed banks one of the two most commonly used methods are the seed extraction method and seedling emergence method, but the combination of the two methods can also be used. In case of the seed extraction method the seeds are extracted from the soil based on their physical characteristics. In the case of extraction by flotation the process uses a salt solution or a specific gravity liquid, in which soil compartments submerge but seeds float on the surface of solution and have to be collected before losing viability (Malone 1967, Roberts 1981, Csontos 2001). Another extraction method is the sieving process, in which case soil samples are washed and sieved in different sized sieves, enabling in this way to dispose of the major soil compartments but retain seeds (Thompson et al. 1997, ter Heerdt et al. 1996, Csontos 2001). A third method, namely the airflow method, uses the air-flow to separate seeds from the soil compartments (Moore & Chapman 1986, Csontos 2001). After the separation seeds are hand sorted, counted and identified under a binocular stereo-microscope and the viability of seeds is tested.

Seeds can be considered as viable if they are healthy, intact and resist a soft pressure (Zelenchuk 1961). This is the easiest method. The TTC-technique uses 2,3,5-triphenyltetrazolium chloride (TTC) to stain metabolically active seed tissues (Lindenbein 1965). In this case only metabolically active seeds can be detected. The detection of dormant seeds is possible using Evans Blue solution (Busso et al. 2015). A third method to determine the viability of seeds is to germinate them. Seeds can be sown or placed into Petri-dishes where appropriate conditions are secured for germination. From the germinated seeds the germination capacity of seeds can be counted (Csontos 2001, Kiss et al. 2018a, Peti et al. 2017). The results of this method can also be elusive because species can have specific germination conditions which have to be met in a germination experiment, if not, species will not germinate. Testing species-specific germination conditions is labour-intensive so data considering this feature of species is scarce. Only two databases contain information about seed germination conditions and germination capacity of wild plant species from Central-Europe flora: SID (RBGK 2018) and HUSEED^{wild} (Peti et al. 2017).

The second major method for seed bank analysis is the seedling emergence method. In this case samples are germinated in greenhouse or in growing chambers. The most commonly used method concentrates the samples by sieving them according to ter Heerdt et al. (1996), eliminating in this way the soil compartments and the major organic material. The concentrated samples are then laid on sterilized soil in germination pots and left to germinate (Csontos 2001). The germination pots are checked regularly; seedlings are identified, counted and removed. In case when identification is not possible seedlings are transplanted to individual pots and grown till identification is possible. The length of the growing period depends on the purpose of the study and can last for years (Csontos 2001). The germination of soil samples without concentration is also a possible way of seedling emergence (Csontos 2001) but is less advised due to the considerably larger sample volume.

Both main methods have their own advantages and disadvantages. The seed extraction method is a relatively fast process with a low place demand and it is a better method to have a clear view of seed bank density. One problem of the method is that seed identification is difficult, and small seeds can be overlooked so species number can be underestimated. The other problem is that without a viability test the viable soil seed density can be overestimated. The identification of seedlings and plants is easier than identifying seeds; thus, the seedling emergence method can give a more precise species number than the seed extraction method. In contrast because of the dormant seeds and the specific germination requirements of species the soil seed bank density can be underestimated using the seedling emergence method (Csontos 2001).

The seed bank ensures the dispersal of species in time and also the preservation of genetic variability of populations (Hong et al. 2012). Studies of seed bank can provide information about the former communities, land use practices, changes of environmental and climatic conditions (Valkó et al. 2011) and also about the past and present degradation level (Hong et al. 2012). By conserving seeds of previous succession phases the seed bank operates as a memento of former communities (Bossuyt & Honnay 2008, Koncz et al. 2011). The seed bank may have importance in habitat restoration, but its role in recovery is often controversial. Some studies claim, that restoration can be based only on the seed bank (Bakker 1989, Plassmann et al. 2009, Wang et al. 2010). Other studies, collected by Bossuyt & Honnay (2008) claimed that seed bank can secure restoration in case when degradation in grasslands occurred less than five years ago. Most studies say, that seed bank alone is not enough for grassland restorations and highlight the importance of restoration activities by propagule input (McDonald 1993, Bossuyt et al. 2006,Blomqvist et al. 2003, Rosef 2008, Stroh et al. 2012).

Grassland restoration

Grasslands are diverse habitats with an exceptional conservation importance. They harbour great species diversity, including both plants and animals (Dengler et al. 2014). Their importance can be highlighted also by the findings of Wilson et al. (2012) and Chytrý et al. (2015). They found world records of plants species at small spatial scales in mesophilous grasslands of the Czech Republic. In the grasslands of the White Carpathians 82 vascular plant species were recorded in 1 m^2 and 109 in 16 m^2(Chytrý et al. 2015). These outstanding species richness scores highlight that the Central-European grasslands are certainly biodiversity hotspots. Beside the importance of grasslands functioning as biodiversity hotspots, they also have importance in the conservation of endemic and endangered species and of specific grassland communities. For example Hungary harbours the 98% of the alkaline grasslands of Europe, which is an important NATURA2000 habitat type (Deák et al. 2014a).

Despite their importance in the conservation of plant and animal species, the species richness and area of grasslands show a declining tendency (Valkó et al. 2012). The reason for this decline are the changes in land use and management practices (Bakker & Berendse 1999, Valkó et al. 2016a), abandonment (Valkó et al. 2018a), urbanization (Hüse et al. 2016, Deák et al. 2016a) and also fragmentation

(Deák et al. 2016b, c, Pullin et al. 2009). The lack of management in grasslands leads to the formation of secondary shrublands and forests (Bakker et al. 1996, Wehn et al. 2017). In Hungary the abandonment resulted in a decline of 14% of grasslands area between 1989 and 2007 (Török et al. 2011, Valkó et al. 2011).

It is highly important to preserve the remained grasslands and also to restore the abandoned and degraded grasslands. The restoration of abandoned agricultural sites is the one of the main habitat-restoration activities in Europe (Cramer &Hobbs 2007). The restoration can rely either on spontaneous succession (Csecserits et al. 2011, Török et al. 2017) or aided by active interventions, like seed sowing, transfer of plant material or community translocation (Deák & Kapocsi 2010, Török et al. 2011, Valkó et al. 2016b, 2018b).

The simplest method is the spontaneous secondary succession (Török et al. 2011). Spontaneous succession is typical in former croplands and it is based on locally available propagules, in the seed bank, seed rain of present species and seed dispersal from adjacent vegetation. The succession is a slow process (Ruprecht 2005), because soil seed bank of target species is generally sparse (Kiss et al. 2016, 2018b, Tóth & Hüse 2014). The result of succession is unpredictable, because weedy, ruderal or invasive species can dominate the seed bank and without further interventions the restored community can differ greatly from the target community (Cseresnyés 2010, Halassy 2001, Török et al. 2014a).

Active restoration can facilitate restoration processes. One of the widely used methods is seed sowing. The seed mixture used can be a low-diversity seed mixture, when the aim is to introduce the 2-8 dominant species of target vegetation to the site; or can be a high-diversity seed mixture, which contains more species (9-40; Deák & Kapocsi 2010) and the aim of using it is to increase species richness and diversity (Török et al. 2011). To increase the chances for successful restoration the use of local ecotypes is advised (Vander Mijnsbrugge et al. 2010), because seeds are already adapted to the environmental conditions of the target site and the chances for genetic incompatibility are lower than in case of seeds originating from commercial sources (Deák & Kapocsi 2010, Török et al. 2011). Propagules can also be introduced via plant material transfer. Fresh plant material, hay or litter can be transferred in cases when the production of a seed mixture would be difficult because of the high number of species. It is important to use material from a donor site in good condition (Scotton et al. 2012). The highest success can be obtained by using fresh plant material between June and August shortly after collecting (Török et al. 2011). Besides its use in species introduction, plant material also protects soil surface from erosion and provides suitable microclimate for germination (Deák & Kapocsi 2010). Another possible but not widely recommended method is topsoil transfer. The success of topsoil transfer is generally low, its costs are extremely high and it also represents a serious damage to the donor habitat (Török et al. 2011).

Restoration projects do not end with the species introduction by seed sowing, plant material transfer or other activities, because post-restoration management is needed to reach and maintain a site in good condition (Kelemen et al. 2014). Mowing and grazing are widely used post-restoration management methods (Tälle et al. 2016), that can remove the accumulated plant biomass and litter, which otherwise would hamper seed germination (Ruprecht et al. 2010, Valkó et al. 2012). Grazing and litter removal can open microsites where new species can establish (Eskelinen &Virtanen 2005, Eichberg & Donath 2017). Grazing animals can also introduce new species (Mann &Tischew 2010, Freund et al. 2014).

Aims of the study

The aim of the dissertation was to test the effects of propagule availability on restoration success, by studying the role of seed bank in grassland recovery and the possibilities to overcome propagule and microsite limitation in restoration projects. This Ph.D. dissertation contains two chapters altogether. Chapters are based on results published in impacted papers of the author. The two chapters concern with different aspects of grassland restoration and management as follows:

*Chapter 1.*The aim of the study was to review studies which examined soil seed bank of grasslands and wetlands across the world and link these studies to climate change so we can make conclusions regarding the potential effects of climate change on the soil seed bank. We reviewed studies which studied the first- and second-order effects (inundation, flooding, fire, drought) of climate change on soil seed bank to evaluate the potential of soil seed bank in buffering climatic extremes and uncertainties. Our model ecosystems were grasslands and wetlands. Our questions were the following: (i) How will the seed bank density and species composition of tropical and temperate ecozones change due to the changes in temperature and precipitation patterns? (ii) Can the soil seed bank of native species buffer the second-order effects of climate change? (iii) Is the native soil seed bank able to support the resilience of actual grassland and wetland communities and also to be the basis of future restoration activities? We also aimed to identify existing knowledge gaps and to highlight the importance of seed bank studies for incorporating native soil seed bank in conservation and restoration projects in changing climate.

*Chapter 2.*In the second study, we tested a novel method to overcome propagule and microsite limitation for restoring the diversity of species-poor grasslands. The aim of the study was to examine the effectiveness of the establishment windows to introduce new, characteristic species to the previously restored species-poor alkaline and loess grasslands in the Hortobágy National Park, East-Hungary. Our questions were the following: (i) Which target species can establish more successfully? (ii) How does the size of establishment windows affect the establishment success of target species and weeds? (iii) How do management types (grazing or non-grazing) affect the species establishment, species composition and community development in establishment windows?

Chapter 1. Role of seed bank in buffering climate change effects in grasslands

Summary

With changing climate the importance of seed banks in the recovery of plant communities is expected to increase. The knowledge about their potential in conservation of plant species is crucial to develop effective conservation and restoration strategies under the changing climate. We conducted a systematic research of seed bank studies, including both field and experimental seed bank studies, to review the potential of seed bank in buffering climatic fluctuations and extremities. In total 42 studies evaluated the first-order or second-order effect of climate change on grasslands soil seed bank. From these studies we concluded that persistent seed bank has the potential to support passive restoration in case of wetlands and frequently disturbed habitats. In other cases, in places where disturbance events were sparse, active intervention by seed addition will be needed. In case of transient species repeated introduction may be the most efficient. Restoration projects have to consider predicted climatic changes and introduce those native species which can tolerate predicted climate changes.

Introduction

Although the seed bank is a widely studied topic, we have limited knowledge about the relation between seed bank and climate change, which can alter highly the structure of seed bank. Different studies aimed to predict future climate changes, which will have different effect in global and in regional scales. The main factors of climate changes affecting plants are the changes in precipitation and temperature patterns worldwide (Arnell 1999, Trenberth 2011). Globally, the surface temperature has increased since the 19th century and this trend will continue, the number of warm days and nights and the length of warm periods will also increase (Stocker et al. 2013). The number of cold days and nights and snowfall events will decrease. An increase in the water temperature of the oceans and higher air humidity was also detected along with decreasing near-surface humidity. In case of precipitation the 'wet-get-wetter' and 'dry-get-dryer' effect will occur (Stocker et al. 2013). Extreme weather conditions, like extreme precipitation or heat events are also likely to occur more often (Stocker et al. 2013).

Great changes are predicted in case of plant communities. The species composition of communities and the abundance of particular species can change in locations, because species may migrate poleward or toward higher altitudes (Walther et al. 2002). Phenotypic plasticity and dispersal ability will have a decisive role in plants survival by buffering changes to some extent (Valladares et al. 2007). Climate-induced changes in plant phenology may result in shifts in germination, flowering and seed maturation periods (Cleland et al. 2007).Species unable to adapt or migrate will face local, regional or even global extinction (Thomas et al. 2004). The synergistic effects of the fast climatic changes, the slow responses of habitat specialist plants and migration barriers in fragmented landscapes all put several plant species at a high risk of extinction. Thomas et al. (2004) claimed that the extinction rate will be higher in case of species with low dispersal ability or species in fragmented landscapes. Based on species-area relationship and the possibility of further habitat loss, as a main threat of species loss, the highest extinction rate is expected in scrublands. Thuiller et al. (2005) considered only European plant-species and forecasted a lower extinction rate but also a high vulnerability. They claimed that most vulnerable are mountain habitats and less vulnerable the southern Mediterranean and a part of Pannonian regions.

Studies aiming to understand the response of aboveground vegetation of plant communities to changing climate are mounting, but few studies focus on soil seed bank. The effect of temperature changes and water supply regimes to seed dormancy and germination was studied by Walck et al. (2011). They reviewed studies of different regions comparing the driving factors of seed dormancy break and germination and the potential effect of climate change to them. In his work Ooi (2012) reviewed studies about the effect of climate change on seed longevity and seedling recruitment. Despite these reviews, the potential of soil seed bank in buffering the effect of climate change and its role in community resistance and conservation is still undiscovered.

Aims of the study

The aim of the study was to evaluate the potential effect of climatic change on soil seed bank in case of grasslands and wetlands by reviewing papers which studied the first- and second-order effects (inundation, flooding, fire, drought) of climatic change on soil seed bank. We wanted to find answers to the following questions: (i) How do the forecasted temperature and precipitation changes affect soil seed bank composition in tropical and temperate ecozones? (ii) Can the seed bank buffer second-order effects, like flooding, drought and fires, of climate change? (iii) Can the soil seed bank support future restoration activities and be a basis of community resilience? We also aimed to identify existing knowledge gaps and also to highlight the potential importance of seed bank concerning conservation and restoration activities in changing climate.

Materials and methods

Using ISI Thompsons Web of Knowledge we searched online literature to find articles about grasslands and wetlands soil seed bank around the world. We used the following keywords: ‘seed bank’ AND ‘grassland’ OR ‘wetland’ OR ‘meadow’ OR ‘steppe’ OR ‘prairie’ OR ‘field’ OR ‘sward’ OR ‘savannah’. We found in total 2,431 articles. We screened the papers by their titles and abstracts, omitted irrelevant studies like single-species studies and considered only the ones which focused on soil seed bank of grassland and wetland communities. We selected in total 308 articles for further evaluation. After the final, detailed evaluation we considered 42 studies, with the following inclusion criteria regarding seed bank data, habitat types and effect of climate change.

We included studies presenting qualitative or quantitative data about the seed bank density and species richness or functional groups of grasslands.

In case of habitat types we considered those conducted in open habitats, namely grasslands, wooded grasslands and wetlands. We categorized the studied habitats into four categories according their moisture regime and geographical position. The four categories were the following: (i) tropical and subtropical wetlands, (ii) temperate wetlands, (iii) tropical and subtropical grasslands and (iv) temperate grasslands.

We included both studies analysing the first-order and second-order effect of climate change on seed bank. Studies which analyse the first-order effect of climate change, i.e. the changes in temperature and precipitation, used experimental climate manipulation treatments. To study the second-order effects of climate change on soil seed bank we included papers which analysed the effect of drought, flooding and fire, important disturbance events which can be altered by changing climate. We did not consider the effect of sea level rise and effect of human activities.

We used predicted climate change scenarios for 2016-2035 time period made by Coupled Model Intercomparison Project Phase 5 (CMIP5; Taylor et al. 2012), where the reference period was 1986-2005. The projections were made under Representative Concentration Pathway (RCP4.5) scenario, using the 50th percentiles (Stocker et al. 2013). According to this scenario we were able to categorize the studied localities into two main scenarios: (i) Increased precipitation in the growing season; (ii) Decreased precipitation in the growing season.

Results

Tropical and subtropical wetlands

We found 4 studies in this category (Table 1). In the studied sites, located in Northern South-America, South and Southeast Asia (Figure 1), a 0.5-1°C temperature increase is predicted, while the amount of precipitation is forecasted to increase by 10%. The studies focused on the flooding effect on grasslands soil seed bank. In the studied sites, according to predicted changes in climate, flooding events are expected to increase.

Table 1. Seed bank studies evaluating first- and second-order effects of climate change in tropical and subtropical wetlands. Numbers refer to numbers on Figure 1. Arrows represent the direction of significant changes in seed density and seed bank species richness. Notations: ~ - not tested/no change; NA - no data.

Tropical and subtropical wetlands						
Prediction: Increased precipitation						
Nr	Reference	Habitat type	Effects of climate change	Species richness	Seed density	Country
1	Bao et al. 2014	inland wetland	flooding	~	↑	Brazil
2	Oliveira et al. 2015	inland wetland	flooding	↑	↑	Brazil
3	Lu et al. 2010	inland wetland	flooding, vertical position	~	~	China
4	Harun-or-Rashid et al. 2009	wet grassland	flooding	↑	~	Bangladesh

The studied ecosystems are flood-dependent ecosystems. Studies conducted in different elevations of wetlands found a high seed bank density in the lowest elevations of wetlands, which are also the wettest parts of the area (Bao et al. 2014, Oliveira et al. 2015). Considering the frequency and duration of flooding studies found that seed density is not affected by these two factors (Lu et al. 2010, Harun-or-Rashid et al. 2009). The findings suggest that changes in frequency and duration of flooding events due to climate change will not damage soil seed bank and these wetland ecosystems can maintain their current species composition. The seed bank contains enough seeds, mostly seeds of flood-adapted species, to re-colonize the sites. In Bangladesh increased flooding frequency may favour grasslands area in expense of mangroves area (Harun-or-Rashid et al. 2009). The seed bank of this area, indifferently of the habitat being grassland, swamp forest or sand dune, is dominated by typical grassland species. Flooding events along with forecasted increased cyclonic events leads to gap formation. In these gaps grassland species can establish from the persistent seed bank while mangrove forest lack persistent seed bank and loss territory. An increase in the area of native grasslands may occur also in the Pantanal wetlands. Here another role of flooding is to suppress the spreading of invasive non-flood-adapted *Urochloa humidicola* (Bao et al. 2014).

Temperate wetlands

We found 11 studies in this category (Table 2). In the study sites the temperature is predicted to increase by 0.5-1.5°C. In case of precipitation in 9 sites, situated in Western-Europe, Southeast-Asia and Eastern North-America, an increased precipitation level is predicted. Only in two sites, located in Central-Europe, a decrease in precipitation is forecasted (Figure 1).

Table 2. Seed bank studies evaluating first- and second-order effects of climate change in temperate wetlands. For notations, please see Table 1.

Temperate wetlands						
Prediction: Increased precipitation						
Nr	Reference	Habitat type	Effects of climate change	Species richness	Seed density	Country
14	Ma et al. 2012	inland wetland	drought, salinization	~	~	China
15	Hong et al. 2012	inland wetland	flooding	NA	~	China
16	Galatowitsch & van der Valk 1996	inland wetland	reflooding	↓	↓	USA
17	van Dijk et al. 2007	wet grassland	reflooding	~	NA	The Netherlands
18	van Duren et al. 1998	wet grassland	reflooding	↓	↓	The Netherlands
19	Bekker et al. 1998	wet grassland	groundwater level	~	~	The Netherlands
20	Lee et al. 2014	inland wetland	flooding	↓	↓	South Korea
21	Herrick et al. 2007	coastal wetland	flooding	↓	↓	USA
22	Kimura & Tsuyuzaki 2011	inland wetland	fire, drought	↑	↑	Japan
Prediction: Decreased precipitation						
23	Hölzel & Otte 2001	wet grassland	flooding	~	↑	Germany
24	Hölzel & Otte 2004	wet grassland	flooding	~	↑	Germany

In 9 of the study sites the potential of soil seed bank in wetland restoration was studied. The most commonly used restoration method in wetlands is rewetting, which means the restoration of former hydrological regime in wetlands (Verhoeven 2014). Previous studies claimed that the seed bank of wetlands contains high-density persistent seeds, especially in sites where unpredictable flooding and drying cycles occur (Brock et al. 2003, Bossuyt &Honnay 2008). In two study sites the reviewed researches found, that rewetting would be enough for wetland restoration without further species introduction. The studied degraded and dried wetlands had proper seed bank species composition for successful restoration (Ma et al. 2012, Hong et al. 2012). This finding suggest that studied wetlands are resilient ecosystems, which can rely on their seed bank even if the future increase in temperature results in the temporary drying out of wetlands due to the evapo-transpiration.

Studies conducted in other wetlands highlighted the importance of species introduction to target sites. In these cases restoration cannot be based only on soil seed bank, because even after rewetting seed banks species richness is low compared to natural wetlands. Especially the seeds of prairie, sedge meadow and submersed aquatic species is lacking from a wetland in North-American prairie (Galatowitsch & van der Valk 1996). Van Duren et al. (1998) and van Dijk et al. (2007) also found, that target species have to be introduced by active restoration, otherwise the structure of the wetland cannot be completely restored due to the lack of characteristic species in the seed bank.

The frequency and durability of floods will also change due to the increased precipitation, which means that floods will be more frequent or will last longer. This may be beneficial for wetland species, according to the results of Bekker et al. (1998b) in Dutch wetlands. The anoxic conditions caused by the high-water level treatment decreased the survival rate of dry grasslands species seeds but wet grassland species had higher survival rate under these condition. Another effect of flooding may be the homogenization of soil seed bank species composition (Lee et al. 2014). Extreme flooding events can damage soil seed bank by decreasing the species richness and density of seeds, removes the seeds of wetland plant species and so allows the establishment of common and ruderal species. The destructive effect of extreme flooding was demonstrated also by Herrick et al. (2007), who studied coastal wetlands and found, that sites diked sites contained higher seed density and species richness than undiked sites exposed to flooding events.

In Central-Europe a decrease in precipitation level is forecasted, which may lead to the decrease of flooding events frequency and durability. The decreased flood duration may result in a decrease in seed bank density in higher-elevated flood meadows, as found in the riverine ecosystems of Rhine valley (Hölzel & Otte 2001). Longer flood duration results the appearance of disturbance-tolerant species in turf gaps. In these ecosystems, according to Hölzel & Otte (2004), persistent seed banks have crucial importance to buffer the variable hydrological conditions typical for flood-meadows of the Rhine valley and so they are also able to buffer forecasted changes in flooding regimes.

The effect of fire, drought and salinization on soil seed bank was studied by two studies. The increased precipitation and water level may decrease the fire severity in a fire-prone swamp located in Japan. This may also result a decrease in species richness, seed density and seed germination (Kimura & Tsuyuzaki 2011), and lead to the exhaustion of soil seed bank and to changes in seed bank and vegetation composition. In some regions the predicted increase in precipitation cannot compensate the evapo-transpiration rate due to increased temperature and this will lead to the drying out and then to the salinization of wetlands (Ma et al. 2012). In the Tibetan plateau due to drought and salinization a species-enrichment of the soil seed bank happened, but the soil still contained typical wetland species for a successful restoration.

Tropical and subtropical grasslands

There were 9 studies in this category (Table 3), where the temperature is forecasted to increase by 0.5-1.5°C. In four of the studied sites, located in the outer parts of the continents, a 10% increase in precipitation level is forecasted, while in five sites, located in inner parts of the continents, the precipitation is forecasted to decrease by 10% (Figure 1).

Table 3. Seed bank studies evaluating first- and second-order effects of climate change in tropical and subtropical grasslands. For notations, please see Table 1.

			Tropical and subtropical grasslands			
			Prediction: Increased precipitation			
Nr	Reference	Habitat type	Effects of climate change	Species richness	Seed density	Country
5	Espinosa et al. 2013	dry shrubland	vertical position	↑	↑	Ecuador
6	Scott et al. 2010	savanna grassland	fire, heat, smoke	↑	↑	Australia
7	Anderson et al. 2012	woody savanna	heat, smoke, precipitation	NA	↑	Tanzania
8	Mamede and de Araújo 2008	woody savanna	fire	↓	↓	Brazil
			Prediction: Decreased precipitation			
9	McLaughlin & Bowers 2007	dry grassland	fire	↓	↓	USA
10	Wright & Clarke 2009	dry grassland	fire, heat, smoke	↑	↑	Australia
11	Williams et al. 2005	savanna grassland	fire, heat, smoke	↓	↑	Australia
12	Gashaw et al. 2002	woody savanna	fire	~	~	Ethiopia
13	de Andrade & Miranda 2014	woody savanna	fire	~	~	Brazil

One of the studies directly compared the seed bank composition of grasslands along an altitudinal gradient having different climate (Espinosa et al. 2013). The temperature and precipitation level showed great differences along in different elevations of the tropical dry scrubland in Ecuador. The species richness and seed density of seed bank was higher in higher altitudinal gradient, which was represented by a higher precipitation level. In this site differences in climate determined the formation of different seed bank species composition, so the climate acted as an environmental filter. Higher altitudes in this case were represented by more favourable conditions for species establishment, survival and reproduction and this leads to increased seed production, seed density and species richness. With an increase of precipitation level conditions may be more favourable also in lower altitudes and an increase in seed density and species richness may occur in these dry tropical scrub ecosystems.

Eight out of the 9 studies evaluated the effect of fire components and fire regimes on the soil seed bank of grasslands. Fire regimes in subtropical and tropical regions will probably change due to the climate change, which will alter the available amount of fuel and will change ignition parameters (Flannigan et al. 2009). Changes in precipitation level will change the amount of fuel. Higher precipitation level could lead to the formation of woody vegetation, or if not possible, to the accumulation of fuel, namely of combustible biomass. Decreased precipitation level may also lead to slower accumulation of combustible plant biomass. Increased temperature may increase the possibility of fire ignition. We did not consider in this case other factors, like land use, fire policy or human population density.

The study sites of the Arizonian dry grasslands and Australian savannas can be characterised by seasonal, well predictable precipitation dynamics. In these dry ecosystems the seed bank is dominated by transient species, while persistent species have only a sparse seed density (McLaughlin & Bowers 2005, Scott et al. 2010). Although transient seed bank strategy is favourable in current conditions, changing climatic conditions may not favour this strategy. Transient species will not be able to cope with predicted changes which lead to increased climatic variability and shifts in suitable growth conditions. The timing of fires in such ecosystems has crucial importance. Scott et al. (2010) examined the effect of different fire intensities on soil seed bank of fire-prone ecosystems of Australian savannas. High fire intensity enhanced the seed germination but low fire intensity not. They also studied the effect of heat and smoke and found that both factors supported seed germination, especially when most of the seeds were in dormant state in course of dry season. The seed bank of Arizonian dry grasslands is composed mainly native species, which have a dense seed bank compared to the burned sites, where fires supported the formation of exotic vegetation and seed bank, but with lower seed density (McLaughlin & Bowers 2005). The restoration of these Arizonian dry grasslands could be only possible by the eradication of exotic species and sowing of native species in several consecutive years.

In other tropical dry ecosystems where fire events and water availability are unpredictable, persistent seed bank has increased importance (Williams et al. 2005, Wright & Clarke 2009, Anderson et al. 2012). As previously mentioned in these ecosystems fire can act as a germination signal for seeds. Especially smoke, one of the fire components supports seed germination and increases germination rate from soil seed bank (Williams et al. 2005, Anderson et al. 2012). In the savannas of the Serengeti National Park, Anderson et al. (2012) found that there is a significant interaction between rainfall and fire: low rainfall sites combined with low fire frequency had lower seed germination than low rainfall sites with higher fire frequency. In the arid Australian savannas Wright & Clarke (2009) found that vegetation and soil seed bank had a low similarity, perennial grasses and woody species of vegetation lacked or had only a sparse soil seed bank. Researchers claimed, that the juxtaposition of fire events and seed rain will determine the grass-woody ratio of site and so, in the long term, the fire regime.

According to the previously mentioned studies we concluded that increased rainfall or fire activity many times is the driver of increased soil seed bank expression in tropical savannas located in the outer parts of the continents (Scott et al. 2010, Anderson et al. 2012). In the Caatinga vegetation in Brazil fires reduced the seed density and species richness of soil seed bank and especially affected grass species seed bank (Mamede & de Araújo 2008). An increase in fire frequency and intensity could lead to an increase of forbs abundance in expense of grasses abundance both in vegetation and soil seed bank. In the Cerrado vegetation in Brazil fire leads to a decrease in monocots seed density one year after the fire, while a threefold increase in seed bank density was detected in case of dicots (de Andrade & Miranda 2014). The different contribution of monocot and dicot species to the seed bank after a fire event show that in fire-management plans not only fire frequency but season also must be considered for successful restoration and maximum seed bank density.

In some of the study sites a decrease in precipitation level is forecasted which may lead to decreased fire activity. In wooded savannas of Ethiopia the precipitation level is forecasted to decrease in the rainy season and to increase in the dry season which may favour species with earlier germination period. Changes in plant phenology can not only alter the germination time of species but may also lead to higher seedling mortality if growing conditions would be not optimal for plant growth (Gashaw et al. 2002). Currently these ecosystems are characterised by frequent but relatively low-intensity fires, which enable the dominance of graminoid species both in vegetation and seed bank. A decrease in fire frequency may reduce the grasslands species abundance in vegetation and soil seed bank, as grassland species are supported by fires and enable the establishment of woody species and the reduction of flammable plant material, as woodlands are less flammable as grasslands.

Temperate grasslands

In total 16 studies were conducted in temperate grasslands (Table 4), where the climate change forecasts a temperature increase of 0.5-1.5°C along with a 10% precipitation increase in sites located in central North-America and in Southeast-Asia and a 10% precipitation decrease in 10 sites located in West- and South-Europe, South-Africa, southern part of South-America and South-Australia (Figure 1).

Table 4. Seed bank studies evaluating first- and second-order effects of climate change in temperate grasslands. For notations, please see Table 1.

Nr	Reference	Habitat type	Effects of climate change	Species richness	Seed density	Country
Temperate grasslands						
Prediction: Increased precipitation						
25	Hild et al. 2001	prairie	drought	NA	↓	USA
26	White et al. 2012	dry grassland	warming, precipitation	~	~	Canada
27	Li et al. 2011	dry shrubland	drought	↓	↓	China
28	Romo & Gross 2011	dry grassland	fire	↑	↑	Canada
29	Ren & Bai 2016	dry grassland	ash, smoke	↑	↑	Canada
30	Abrams 1988	prairie	fire	~	↓	USA
Prediction: Decreased precipitation						
31	Akinola et al. 1998	dry grassland	warming, drought	NA	~	United Kingdom
32	del Cacho et al. 2012	dry shrubland	warming, drought	NA	↓	Spain
33	Figueroa et al. 2004	dry shrubland	fire	~	↑	Chile
34	Gonzalez & Ghermandi 2008	dry grassland	fire	↑	↑	Argentina
35	Ghermandi & Gonzalez 2009	dry grassland	fire, drought	NA	↓	Argentina
36	Ghermandi et al. 2013	steppe	fire	↓	↓	Argentina
37	Fernández et al. 2012	dry shrubland	fire	~	↑	Spain
38	Heelemann et al. 2013	renosterveld	smoke	~	↑	South African R.
39	Snyman 2013	dry grassland	fire	NA	↑	South African R.
40	Ghebrehiwot et al. 2012	mesic grassland	fire, heat, smoke	~	~	South African R.
41	Wills & Read 2007	heathland	fire, heat	↑	↑	Australia
42	Morgan 1998	dry grassland	fire	~	↓	Australia

Four studies out of the 16 examined the first-order effects of climate change on soil seed bank of temperate grasslands by experimental warming and water/precipitation manipulation. Akinola et al. (1998) used experimental soil warming and water deficit treatments in a British upland calcareous grassland over six years to mimic predicted climatic changes. The experiment had only minor effect of soil seed bank and affected only three species. In contrast Hild et al. (2001) found in a mixed-grass rangeland of North-America that the total seed bank density decreased due to experimentally induced drought. Water deficit had especially negative effect on cool-season annual grasses. White et al. (2012) found in a Canadian dry grassland, that warming had no effect on soil seed bank density but reduced precipitation level increased the similarity between the composition of soil seed bank and aboveground vegetation. The forecasted increase in precipitation level in the previous two study sites may have the opposite effect on soil seed bank than found in studies, so it will positively affect the seed density. In the Mediterranean region decreasing precipitation level may lead to reduced seed density, according to a 9-year-long climate manipulation study conducted in a scrubland (del Cacho et al. 2012). The study also found that open microsites are more affected by drought and warming caused by climate change than closed microsites, in which case shrub canopy act as a refuge site for many species and also provide suitable conditions for species survival. The results suggest that in Mediterranean scrublands total seed bank density and the seed density of short-lived species will decrease under drought conditions.

The remaining studies conducted in the temperate grasslands evaluated the effect of drought and fire on soil seed bank. Forecasted precipitation increase is the driver of seed density increases in dry valleys of China and also of increases the species richness (Li et al. 2011). Increased precipitation level may also increase plant biomass production in North-American prairies (Flannigan et al. 2009). The increased amount of plant material will alter the frequency, intensity and durability of both wildfires and human induced fires (Valkó et al. 2014b). In North America, in the northern edge of a Fescue Prairie of the Great Plains, Romo & Gross (2011) found, that fire affected positively the seed bank density, species diversity and evenness of species one year after the fire, but with time this effects diminished. A study conducted by Ren & Bai (2016) in the same region proved that ash and smoke, both fire components, propmoted native forb species, which means that their species richness in seed bank and also their density in seed bank will increase with increasing fire frequency. Altough fire can increaseseed bank density and richness, too frequent fires like annual fires may negatively affect the soil seed bank, as found in the Kansas Prairie (Abrams 1988).

In sites where a decreased precipitation level is forecasted the major limitating factor of grassland restoration from soil seed bank will de drought. The possible decreasing fire frequency and intensity due to lack of combustible biomass negatively affects the Chillean matorral dry shrublands, where most species harbour only transient seed bank. Decreasing fire frequency result decreasing seed density, especially in case of annual grass species (Figueroa et al. 2004). The changes in fire parameters will also affect the dry grasslands in Argentina, where the lack of fire may negatively affect the soil seed bank density and species richness, especially the seed bank of annual species. Perennials will benefit from the decreased fire frequency (Gonzalez & Ghermandi 2008). Ghermandi & Gonzalez (2009) also found that in Patagonia dry grasslands low-severity fires were beneficial for the fire-adapted short-lived species which produce numerous and long-term perisitent seeds. Previous studies proved that fire can act as an important driver of community diversity by creating gaps makes possible the germination and survival of gap-stategist species. Althought fire has these positive effects, high-severity fires can be detrimental even to the fire-adapted short-lived species and support the establishment of exotic species (Ghermandi et al. 2013).

Decreased fire activity will have major negative effect in fire-prone ecosystems. Fernández et al. (2012) found in the Spanish gorse shrublands that wildfires had positive effect on soil seed density and induced germination while species richness was not affected. Similar patterns were observed in the Mediterranean region of South-Africa by Heelemann et al. (2013). Snyman (2013) proved that despite the seemingly positive effect of fire one year after the fire event to the seed bank of semi-arid South-African rangelands, in long-term it will negatively affect disturbance-sensitive species but will favour species of degraded habitats. The disappearance of species unable to tolerate disturbance will result in a decrease in seed bank density and diversity. However, the seed bank will probably remain stable in case of disturbance-tolerant species. The smoke component of fires is proved to be an important driver of seed germination in case of grass and forb species in mesic grasslands of South-Africa (Ghebrehiwot et al. 2012). In the lack of fires in this sites smoke treatment could be used in restoration activities of degraded lands to induce seed germination. Not only the smoke, but also the heat component of fires effects positively the seed density, as found in study sites of southern Australia (Wills & Read 2007). A further effect of decreasing fire frequency is the increased seed bank density of exotic species and native perennial species (Morgan 1998).

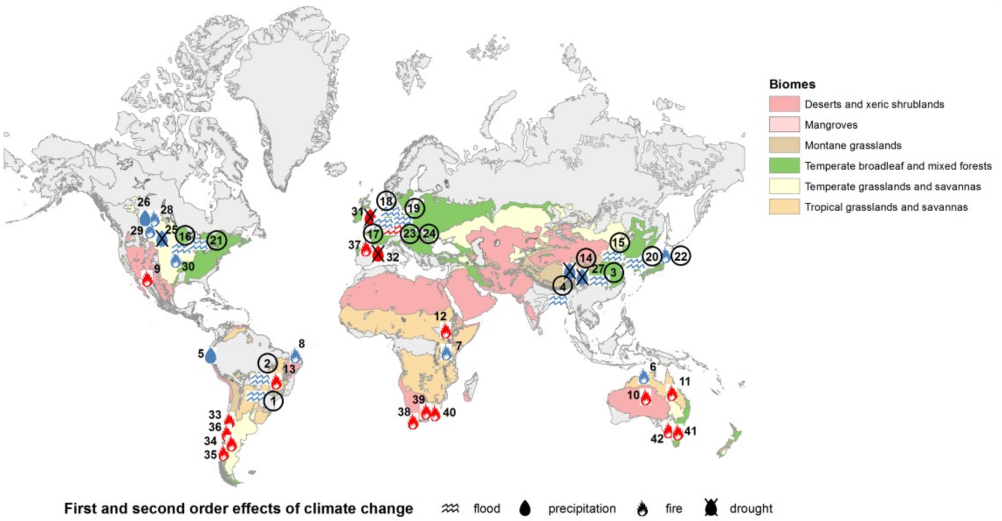

Figure 1. The location of studied sites and regions included in the systematic review. Numbers correspond to the study numbering in Tables 1-4. Wetlands are marked with a circle. Notations for colours of climate change prediction symbols: blue symbols: increased precipitation is forecasted in the study site; red symbols: decreased precipitation is forecasted in the study site. Biomes not covered by our study are marked with grey.

Discussion

Although we found studies from all continents about the first- and second-order effects of climate change on seed bank (Figure 1), many regions still lack such studies (Central-America and Caribbean, East-, West- and Central-Asia, Pacific Islands region, polar regions). Thus, the existing studies represent only a minor part of the continents. Most studies of wetlands studied the potential effect of changes in flooding parameters or the effect of drought, giving a proper view about the potential changes in case of precipitation decrease or increase. In case of grasslands the fire induced changes were mostly studied. Only four studies studied directly the effect of climate change by experimentally manipulating precipitation regimes and temperature. Not only there are few studies about the direct effect of climate change to soil seed bank but regional scenario-based approaches are also missing despite the fact, that these studies would be crucial to properly design suitable long-term grassland conservation and restoration projects which also consider the possibility in changing target vegetation.

The reviewed studies prove that changing climate will have major effects on soil seed bank either by its firs-order or by second-order effects (Figure 2). Acting as an environmental filter it will change both the composition and density of soil seed bank of grasslands and wetlands. Precipitation proved to be the driving of seed bank density increase (Hild et al. 2001, White et al. 2012, Espinosa et al. 2013). The soil seed bank will undergo greater changes in case of historically stable habitats. Sites with harsh and unpredictable environmental conditions possess persistent seed bank. In such sites climate change will benefit those native species which are already adapted to disturbances and to the unpredictable availability of resources. It seems that in case to determine the grasslands resilience based on soil seed bank will have to take into consideration the historical disturbance regime of the given habitat. Habitats with severe, unpredictable or frequent disturbances can regenerate from the persistent seed bank of species. Such disturbance-affected habitats are flooded wetlands (Bao et al. 2014, Oliveira et al. 2015) or fire dependent ecosystems (Wright &Clarke 2009, Anderson et al. 2012, Williams et al. 2005), which in the future may be able to buffer changes in disturbance regimes caused by climate change and to recover from persistent seed bank. In contrast to disturbed habitats, relatively stable habitats, characterised by less severe and predictable disturbances, most species do not have persistent seed bank and rely on transient seeds (McLaughlin & Bowers 2005, Scott et al. 2010). Such ecosystems cannot cope with the changing climate, soil seed bank cannot buffer climatic changes. These ecosystems, like non-fire-prone temperate grasslands, will undergo major changes.

It is important to mention that both increased and decreased disturbance severity and frequency leads to directional and irreversible changes in the structure of grassland

and wetland communities by changing the species composition and seed density of the soil seed bank.

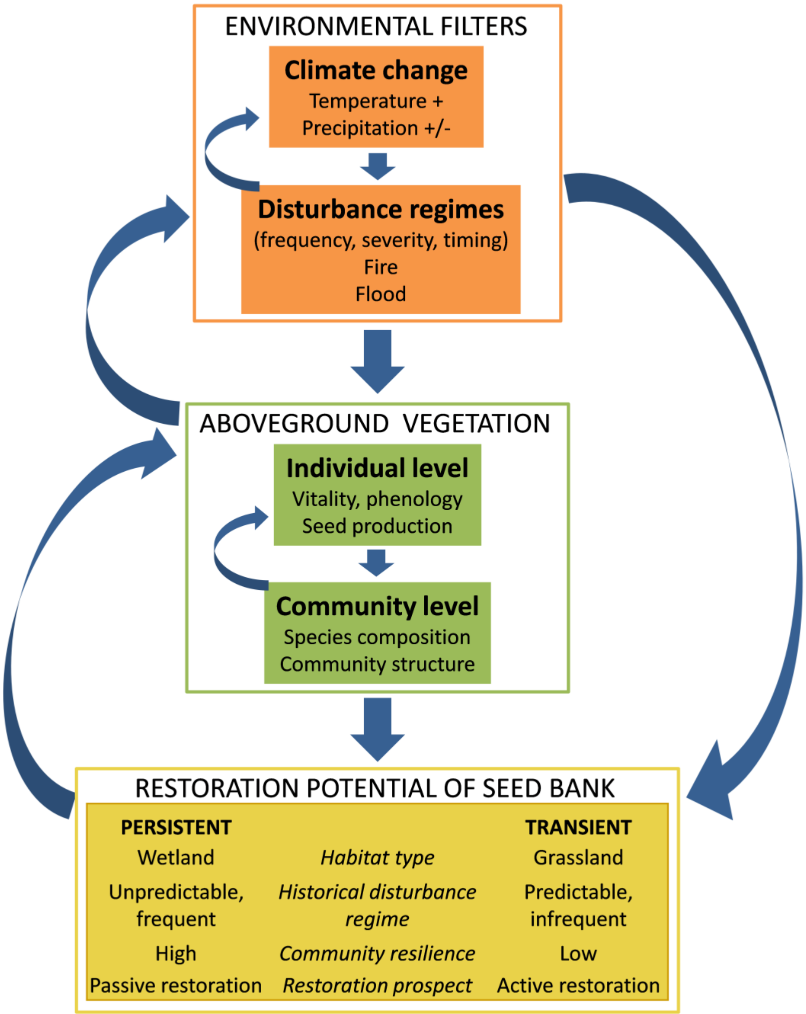

Figure 2. Flow chart presenting the relationship between climatic changes, disturbance regimes, aboveground vegetation, and the restoration potential of seed bank.

We conclude that active restoration by propagule introduction will have increased importance in stable habitats affected by less disturbance and characterised by transient seed bank. The restoration projects should introduce native species which can tolerate forecasted climatic changes. In historically disturbed habitats passive restoration can be based on persistent seed bank.

Chapter 2.Establishment windows – A tool to enhance grassland biodiversity

Summary

Conservation of existing grasslands, maintaining and halting the loss of their biodiversity together with the restoration of degraded ecosystems are of crucial importance in the EU Biodiversity Strategy. One widely-used method is low-diversity seed mixture sowing, which is recognized for its high predictability and fast, promising results. This seed mixture generally contains seeds of a few perennial grasses and according to previous studies can establish within a short time after sowing, can successfully supress weeds and create a dense sward (Török et al. 2010, Deák et al. 2011). The low-diversity seed mixtures are able to restore species-poor grasslands, but forming a dense sward grass species hamper the colonisation and establishment of new, characteristic grassland forbs. The aim of the study was to test the use of a new approach in increasing species-diversity in species-poor grasslands. For the study we selected eight restored grassland sites which were sown by low-diversity seed mixtures eight years before the study. We created four establishment windows in each grassland site by sowing seed mixtures of 35 species into the openings created in the closed grass sward. In the following two years after sowing we monitored and noted the cover of species present in windows, including both sown and non-sown species. We investigated which species are the most successful and can establish rapidly in the windows. We also evaluated the effect of the size (1 m^2, 4 m^2 and 16 m^2) and management type (grazed/unmanaged) of establishment windows by comparing the establishment success of target species and the abundance of weeds. According to our results establishment window sown by high-diversity seed mixtures are able to overcome propagule and microsite limitation. The use of high-diversity seed mixtures enables the successful introduction of target species. All sown species were found in at last one of the establishment windows. Most species had stable cover values between years, and some species became even more abundant for the second year. Less target species with lower cover were characteristics of smaller windows, where we also found stochastic development compared to the larger windows. The cover of sown species and weeds were similar in managed and unmanaged windows. Weed species were present in both study years but their cover was moderate and decreased to the second year. We concluded that establishment windows can act as biodiversity hotspots and in restoration projects larger windows are recommended to be used. Despite the fact that we found no difference between grazed and non-grazed windows, extensive grazing may have importance in dispersal of species and microsites creation on the long run.

Introduction

Natural and semi-natural grasslands are the home of many species in such extent that they can function as biodiversity hotspots. The species diversity of grasslands and also the habitat itself is endangered by both the changing land management practices and abandonment. The intensification of agricultural practices occurs worldwide (Tilman 1999). Many grasslands are turned into croplands resulting in a serious area loss of natural grasslands, alongside with fragmentation, degradation and species diversity loss (Foley et al. 2005, Valkó et al. 2012, 2016a, Deák at al. 2016b). The total lack of management also leads to the loss of grasslands area and biodiversity, because secondary shrublands and forest form in place of grasslands (Milberg 1995, Bakker et al. 1996, Wehn et al. 2017).

One of the targets of the EU Biodiversity Strategy (European Commission 2011) is the regeneration and restoration of degraded habitats and the halting of loss of biodiversity. The conservation of biodiversity by the use of traditional land use regimes could contribute to the conservation of species diversity (Babai &Molnár 2014, Szilassi et al. 2017). Degraded areas, like former croplands, provide a good opportunity for grassland restoration which enables the increase of biodiversity and also offers further ecosystem services like soil protection, weed control and pollination (Tallis et al. 2008). A frequently used active restoration method is seed sowing, when the propagules of target species are introduced to the target area (Deák & Kapocsi 2010, Török et al. 2011). The method is fast, predictable and provides good results (Török et al. 2010, Kiehl et al. 2010,), but it has a major practical drawback, which is the limited access topropagule sources. Well-developed systems secure the availability of seeds of target species of local provenance for restoration projects in countries like Australia, Germany and Switzerland (Scotton et al. 2012). These seeds are available in market. In other countries including Hungary, however, only few species seeds are present in the market. The few forb species available to buy are not from local sources (Tischew et al. 2011, Kirmer et al. 2015). Forsuccessful restoration projects the use of local species seeds is needed which increases the chance of success, because species are already adapted to local conditions and can germinate and establish more successfully than „stranger" seeds (Bischoff et al. 2010, Vander Mijnsbrugge et al. 2010). Because getting seeds is not simple the use of low-diversity seed mixtures is generalised in large-scale restoration projects in several parts of Central Europe (Deák & Kapocsi 2010, Török et al. 2010). The fast forming dense canopy however is species-poor and also halts the establishment of new species by decreasing available sites (Conrad & Tischew 2011, Kelemen et al. 2014). Not only microsite-limitation can be a problem, but also propagule limitation, when target species cannot occur naturally because they are not present in the surroundings of restored area so there is no propagule source

(Moore & Elmendorf 2006). Factors like litter accumulation, low-density seed bank or low seed rain also halt the establishment of new species (Deák et al. 2011, Ruprecht & Szabó 2012, Sengl et al. 2015). Moreover seed banks in ex-arable fields are generally dominated by arable weeds (Hutchings & Booth 1996, Bekker et al. 1997, Halassy 2001, Török et al. 2012, Kiss et al. 2016) and in the intensively used agricultural landscape few natural or semi-natural grasslands remained, which enable only a limited spatial dispersal of target species (Deák et al. 2016c). The low dispersal ability of target grassland species also halts their establishment (Bakker & Berendse 1999, Stampfli & Zeiter 1999, Novák & Konvička 2006).In such cases active restoration is the only way for the target species establishment and for the improvement of biodiversity (Valkó et al. 2018). In active restoration projects artificial openings on the closed sward mimics the effect of droughts, wildfires or animals (Bullock et al. 1995, Zimmermann et al. 2014, Valkó et al. 2014b) and results in a decreased biomass of competitive grasses and also provides the optimal conditions for grassland forb species establishment. The use of high-diversity seed mixtures after the disturbance on the soil surface decreases the chances of failure and promotes target species establishment (Kirmer et al. 2012).

Aims of the study

The aim of the study was to test the effectiveness of the so-called establishment windows in introducing specific species into species-poor restored alkaline and loess grasslands. Our questions were the following: (i) Which are the most successful target species in establishment? (ii) Are there differences between the size of establishment windows in case of the establishment success of target species and amount of weeds? (iii) How does management affect species establishment and species composition is establishment windows?

Materials and methods

Study site

The study was conducted within the ProSeed DBU project in restored alkaline and loess grasslands in East-Hungary, in the Hortobágy National Park, near the towns Egyek and Tiszafüred (Török et al. 2010, Valkó et al. 2016b). The site has continental climate with 550 mm mean annual precipitation and 9.5 ºC mean annual temperature with high interannual fluctuations. It is elevated at 88–92 m a.s.l.(Lukács et al. 2015). The natural vegetation of the site consists of *Beckmannion eruciformis* Soó 1933alkaline meadows (Deák et al. 2014b) and *Bolboschoenetalia maritimi* Hejný in Holub et al. 1967alkaline marshes (Deák et al. 2014c, 2015a) in lower elevations *Artemisio-Festucetalia pseudovinae* Soó 1968alkaline dry grasslands (Valkó et al. 2014b, Deák et al. 2014a) at higher elevations and *Festucion rupicolae* Soó 1940loess grasslands in the most elevated plateaux (Deák et al. 2014a, Tóth & Hüse 2014). In the middle of the 19th century the region was included in agriculture for crop production which resulted in the ploughing of the majority of loess grasslands and many alkaline grasslands as well (Valkó et al. 2016c). After the abandonment of agricultural practices the site underwent a complex landscape rehabilitation in the frame of the LIFE Nature project called 'Grassland restoration and marsh protection in Egyek-Pusztakócs' (project ID: LIFE-04-NAT-HU-119). For restoration low-diversity seed mixtures were sown on former croplands in October 2005 to reintroduce the most important native alkaline and loess grasslands species. The project was one of the largest grassland restoration projects in Europe where approximately760 hectares of grasslands were restored. In the project in lower lying croplands (under 90 m a.s.l.) alkaline seed mixtures of two matrix grasses (*Festuca pseudovina* and *Poa angustifolia*) were sown while in elevation higher than 90 m a.s.l. loess seed mixtures of three matrix grasses (*Bromus inermis*, *Festuca rupicola* and *Poa angustifolia*) were sown. The seeds were sown at a rate of 25 kg/ha. Between 2006 and 2008 the restored sites were mowed once in a year in June and from 2009 extensive cattle grazing was introduces to the site. The dense canopy successfully supressed weed species but the target forb species number and cover remained low (Török et al. 2010, Kelemen et al. 2014).

Seed mixture and establishment windows

The high-diversity seed mixture was formed by 35 native species (Table 5) originating from local sources, collected in the summer of 2013. Collected seeds covers a wide range of species of alkaline and loess grasslands. After collection seeds were air-dried and hand-cleaned. Three replicates of 100 seeds were counted using a SARTORIUS 1702 type balance. Seed mixtures were prepared by mixing all cleaned species seeds, calculated for a sowing rate of 10 g/m². Mixing seeds with soil before sowing prevented the wind to blow them away.

Table 5. The species composition of the high-diversity seed mixtures together with thousand-seed weights and number of seeds sown per m^2.

Species	seed weight (g/1000 seeds)	seeds/m^2
Achillea collina	0.08	685.06
Aegilops cylindrica	35.37	22.70
Agrimonia eupatoria	20.87	44.85
Agropyron cristatum	1.48	160.94
Allium scorodoprasu	16.14	20.37
Aster tripolium ssp. pannonicus	0.48	260.57
Atriplex littoralis	3.27	42.02
Atriplex tatarica	3.17	107.31
Bunias orientalis	43.01	21.28
Bupleurum tenuissimum	1.03	48.15
Carthamus lanatus	16.52	21.38
Centaurea jacea ssp. *angustifolia*	1.16	71.54
Centaurea scabiosa	2.60	89.21
Centaurea solstitialis	1.49	40.25
Dianthus pontederae	0.49	138.13
Falcaria vulgaris	0.62	485.36
Filipendula vulgaris	1.35	863.44
Galium verum	0.27	1654.91
Hypericum perforatum	0.12	464.07
Lathyrus hirsutus	27.43	18.61
Lathyrus tuberosus	31.15	33.66
Lotus corniculatus	1.38	153.42
Plantago media	0.28	171.33
Podospermum canum	3.51	21.46
Potentilla argentea	0.09	607.24
Rapistrum perenne	4.13	9.24
Salvia verticillata	0.49	39.67
Scabiosa ochroleuca	1.22	48.02
Securigera varia	4.59	83.73
Silene viscosa	0.20	164.11
Silene vulgaris	0.60	284.01
Trifolium angulatum	0.44	752.68
Trifolium campestre	0.22	155.86
Trifolium retusum	0.45	154.81
Trifolium striatum	2.33	91.52

Eight restored sites were selected in the restored area, four in restored sites sown by alkaline seed-mixture and four with loess seed-mixture. In October 2013 four windows were established in every selected site. Window establishment included soil preparation by digging and rotary hoeing followed by raking, which resulted a fine seedbed. The windows had different size: (i) 1 m × 1 m (10 g seed mixture), (ii) 2 m × 2 m (40 g seed mixture) and (iii) 4 m × 4 m (160 g seed mixture). The windows were at least to 50 m from each other to avoid propagule dispersal between them. We used two 4 m × 4 m windows, one was fenced and one was grazed. Smaller windows were also grazed by extensive cattle grazing, stocking rate being 0.5 livestock units per hectare, starting from late April until late October every year. The fenced windows remained unmanaged. In June 2014 and 2015 we recorded the vegetation cover of total biomass and also the percentage vegetation cover of vascular plant species in each window. Nomenclature follows Király (2009).

Statistical analyses

We classified weed species following Török et al. (2012). Adventive species, ruderals and weeds were all considered weeds (Borhidi 1995).

The differences in cover scores of sown species in the first and second year in the four window types was compared with paired *t*-tests (Zar 1999). With linear regression we tested the relation between the frequency and cover of sown species between years. Using linear mixed-effect models (LMEs, Zuur et al. 2009) we tested the effect of 'window size' (fixed factor), year (fixed factor), 'vegetation type' (fixed factor) and 'site' (random factor nested in 'vegetation type') on the vegetation characteristics (dependent variables). Using LMEs in 4 m × 4 m windows we tested the effect of management type (grazed *vs* fenced; fixed factor), year (fixed factor), vegetation type (alkaline or loess seed mixture, fixed factor) and site (random factor nested in vegetation type) on vegetation characteristics (dependent variables). The vegetation characteristics were the following: total vegetation cover, cover of sown species, cover of sown perennial species, cover of matrix grasses (grass species presentin the low-diversity seed mixtures sown during the landscape-scale restoration project) and cover of weeds. We calculated LMEs in SPSS 22.0. Using DCA ordination based on specific cover scores we compared the species composition of the grazed windows and also the species composition of grazed and non-grazed windows. We calculated the DCA ordination in CANOCO 5.0 (ter Braak& Šmilauer 2012).

Results

In total 149 species were detected in the establishment windows. All sown species were found in the two years in at last one of the establishment windows, 31 were recorded in the first year and 34 in the second one. In total 114 unsown species were recorded in the first and second years, 80 in and 91 respectively, out of which 60 species were weeds. The most common perennial weeds in the first year were *Cirsium arvense* and *Convolvulus arvensis*, with mean cover scores of 5.4% and 5.0% respectively. The most common short-lived weeds were *Polygonum aviculare* (4.6%), *Setaria glauca* (2.7%), *Tripleurospermum perforatum* (1.3%), *Bilderdykia convolvulus* (1.5%), *Crepis tectorum* (0.9%), *Stachys annua* (0.9%), *Cynoglossum officinale* (0.6%) and *Capsella bursa-pastoris* (0.3%). In the second year *Convolvulus arvensis* (3.2%), *Cirsium arvense* (2.9%) and *Taraxacum officinale* (2.5%) were the most common perennial weeds while the most common short lived weeds were *Capsella bursa-pastoris* (2.8%), *Bromus tectorum* (1.0%), *Tripleurospermum perforatum* (0.9%), *Cynoglossum officinale* (0.7%), *Stellaria media* (0.5%), *Thlaspi arvense* (0.4%), *Anthemis arvensis* (0.3%) and *Descurainia sophia* (0.3%).

Sown species establishment

Sown species cover between the two years can be characterised by strong positive correlation (linear regression, $R = 0.953$, $p < 0.001$). The frequency of sown species was also positively correlated between years ($R = 0.670$, $p < 0.001$). In most cases there were no significant differences in species cover between the years. *Dianthus pontederae* increased its cover from the first year to the second one in all window types. *Allium scorodoprasum*, *Centaurea sadleriana*, *Galium verum*, *Plantago media*, *Podospermum canum* and *Silene viscosa* increased cover in at least one type of window. *Carthamus lanatus* hadincreased cover in grazed windows and decreased cover in fenced, non grazed 4 m × 4 m windows. *Aegilops cylindrica* cover decreased significantly in the second year in the 1 m × 1 m sized windows and in the 4 m × 4 m sized fenced windows (Table 6).

The DCA ordination (Figure 3) clearly separates the vegetation of the two years. Most species were plotted toward the second year. The first year's vegetation was characterised by short-lived sown species specific of alkaline grasslands, like *Aegilops cylindrica*, *Atriplex tatarica*, *A. litoralis* and *Bupleurum tenuissimum*. Loess species and almost all perennial species, like *Achillea collina*, *Centaurea jacea* ssp. *angustifolia*,*C. sadleriana*, *Filipendula vulgaris* and *Galium verum* were characteristic for the second year.

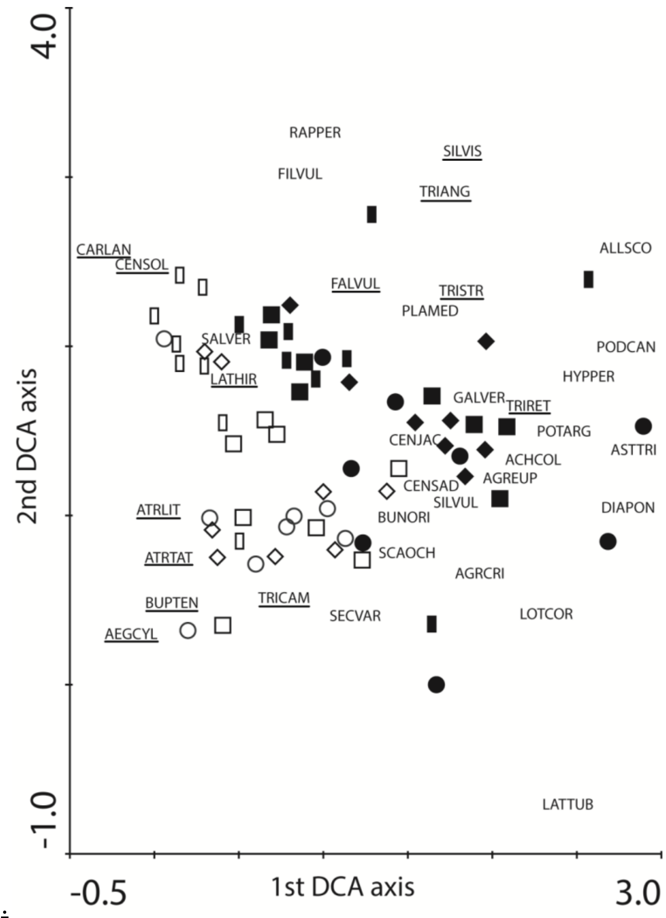

Figure 3. Species composition in the first and second year in the establishment windows plotted by a DCA based on specific cover scores. Notations: ○ – 1×1 m grazed establishment windows, year 1; ● – 1×1 m grazed establishment windows, year 2; □ – 2×2 m grazed establishment windows, year 1; ■ – 2×2 m grazed establishment windows, year 2; ◇ – 4×4 m grazed establishment windows, year 1; ◆– 4×4 m grazed establishment windows, year 2; ▯ – 4×4 m fenced establishment windows, year 1 and ▮ – 4×4 m fenced establishment windows, year 2. We gave the first three letters of the genus and species names of the 35 sown species. Short-lived species are <u>underlined.</u>

Table 6. Mean cover scores (%) of sown species in the four types of establishment windows in the first and second year compared by paired t-tests. Only species that had significantly increased (↑) or decreased (↓) in at least one type of establishment windows are listed. Significant changes in cover scores are marked by boldface.

Gap type	1×1 m grazed			2×2 m grazed			4×4 m grazed			4×4 m fenced		
Year	Year 1	Year 2	*p*	Year 1	Year 2	*p*	Year 1	Year 2	*p*	Year 1	Year 2	*p*
Aegilops cylindrica	**1.5**	**0.2**	**0.010 ↓**	3.1	0.4	0.083	2.4	0.8	0.119	**5.3**	**0.1**	**<0.001 ↓**
Allium scorodoprasum	–	**0.1**	**0.019 ↑**	–	0.1	0.234	–	**0.2**	**0.038 ↑**	–	**0.1**	**0.019 ↑**
Carthamus lanatus	0.1	–	0.442	0.3	0.2	0.878	**0.2**	**0.6**	**0.038 ↑**	**1.6**	**0.1**	**<0.001 ↓**
Centaurea sadleriana	0.8	0.5	0.959	1.6	1.8	0.878	**1.5**	**4.5**	**0.019 ↑**	1.6	1.1	0.574
Dianthus pontederae	–	**0.5**	**0.050 ↑**	**0.1**	**1.6**	**0.050 ↑**	**0.1**	**3.5**	**0.050 ↑**	**0.1**	**0.9**	**0.050 ↑**
Galium verum	1.5	4.0	0.353	1.8	4.0	0.234	2.4	5.3	0.087	**0.9**	**2.3**	**0.050 ↑**
Plantago media	0.2	0.8	0.721	**0.3**	**1.2**	**0.050 ↑**	0.4	1.6	0.130	**0.1**	**1.2**	**0.050 ↑**
Podospermum canum	–	0.1	0.645	**0.1**	**0.5**	**0.038 ↑**	0.2	0.7	0.063	–	0.1	0.234
Silene viscosa	–	–	–	–	0.4	0.090	–	**0.5**	**0.010 ↑**	–	**1.1**	**<0.001 ↑**

Table 7. Species groups cover (%, mean ± standard error) in the first and second year after sowingin the four types of establishment windows.

	Year 1				Year 2			
Window type	1×1 m grazed	2×2 m grazed	4×4 m grazed	4×4 m fenced	1×1 m grazed	2×2 m grazed	4×4 m grazed	4×4 m fenced
Total cover	60.6 ± 5.7	65.6 ± 3.3	74.1 ± 2.3	80.4 ± 2.6	68.8 ± 8.4	76.8 ± 2.9	74.6 ± 3.1	79.4 ± 3.6
Sown cover	28.6 ± 6.0	38.6 ± 4.5	51.8 ± 7.0	66.3 ± 5.5	30.9 ± 8.6	15.8 ± 1.1	59.2 ± 6.8	50.8 ± 10.3
Sown perennial cover	11.7 ± 4.0	18.7 ± 5.0	24.5 ± 5.1	8.2 ± 2.2	20.0 ± 6.4	25.4 ± 3.6	42.9 ± 7.7	20.7 ± 5.0
Matrix grass cover	4.8 ± 2.2	3.7 ± 0.9	2.2 ± 0.3	1.6 ± 1.0	9.6 ± 2.7	6.9 ± 1.6	7.2 ± 1.2	8.1 ± 3.5
Weed cover	26.0 ± 4.0	29.2 ± 5.6	30.7 ± 4.6	18.5 ± 4.4	19.3 ± 6.2	16.2 ± 4.8	23.3 ± 3.3	19.2 ± 7.8

Effect of window size

Window size had significant effect on the total cover of vegetation, the cover of sown species and the cover of sown perennial species (Tables 7 and 8). In both years sown species and sown perennial species reached the highest coves scores in the largest establishment windows. Sown perennial species cover, the total vegetation cover and the cover of matrix grasses increased between the years. Window size had no effect on the cover of matrix grasses. Vegetation type affected only the cover of matrix grasses. Matrix grasses reached a higher cover in sites restored with loess seed mixture. Weeds cover was similar in the windows types but decreased to the second year (Table 7).

Table 8. The effect of 'window size' (fixed factor), 'year' (fixed factor), 'vegetation type' (alkali or loess grass seed mixture, fixed factor) and 'site' (random factor nested in 'vegetation type') on the cover of species groups in the grazed establishment gaps tested by linear mixed-effects models (LMEs). Significant differences are marked with boldface.

	Window size		Year		Vegetation type		Site	
	F	*p*	F	*p*	F	*p*	F	*p*
Total cover	**3.31**	**0.048**	**4.41**	**0.043**	0.30	0.606	**4.85**	**<0.001**
Sown cover	**8.65**	**<0.001**	1.63	0.210	2.35	0.176	1.44	0.226
Sown perennial cover	**8.18**	**0.001**	**9.25**	**0.004**	0.93	0.371	**3.95**	**0.003**
Matrix grass cover	1.58	0.219	**13.35**	**<0.001**	**7.97**	**0.030**	1.40	0.241
Weed cover	0.68	0.511	**6.64**	**0.014**	0.46	0.524	**2.56**	**0.036**

The DCA ordination (Figure 3) found that the species composition of different window sizes was similar in Year 1. In the Year 2 similarity decreased in the smallest grazed windows and increased in the larger windows. Species composition between years was more similar in larger windows than in the smallest ones.

Effect of grazing

Grazing reduced the total vegetation cover of 4 m × 4 m windows and increased the sown perennials cover (Table 9). The total sown species cover, the cover of matrix grasses and cover of weeds was not significantly different between grazed and fenced windows. The matrix grasses cover and the perennial sown species cover showed an increase between the years in both grazed and fenced windows.

According to the DCA ordination (Figure 3) sown short-lived prickly sown species characterised the fenced windows in the first year, i.e. *Carthamus lanatus* and *Centaurea solstitialis*. In the second year sown short-lived non-prickly species, such as *Falcaria vulgaris, Silene viscosa*, *Trifolium angulatum* and *T. striatum.*characterised the fenced windows. The species composition of grazed plots showed lower dissimilarity than the fenced plots in the second year.

Table 9. Effects of 'management type' (grazed/fenced, fixed factor), 'year' (fixed factor), 'vegetation type' (alkali or loess grass seed mixture, fixed factor) and 'site' (random factor nested in 'vegetation type') on the cover of species groups in the grazed and fenced 4×4 m-sized establishment windows, tested by linear mixed-effects models (LMEs). Significant differences are marked with boldface.

	Management		Year		Vegetation type		Site	
	F	*p*	F	*P*	F	*p*	F	*p*
Total cover	**4.31**	**0.049**	0.01	0.926	0.02	0.902	2.13	0.091
Sown cover	0.17	0.687	0.30	0.587	0.71	0.433	1.61	0.190
Sown perennial cover	**19.15**	**<0.001**	**12.22**	**0.002**	1.63	0.249	2.55	0.050
Matrix grass cover	0.01	0.930	**10.94**	**0.003**	1.57	0.257	1.59	0.198
Weed cover	3.10	0.092	0.53	0.474	0.04	0.842	2.55	0.051

Discussion

Establishment success of species

Using high-diversity seed mixtures can enable the establishment of multiple target grassland species at the same time, successfully overcoming propagule limitation (Lepš et al. 2007, Kirmer et al. 2012, Prach et al. 2013). But despite the availability of seeds, successful colonization can still be hampered by microsite limitation in longer time periods (Öster et al. 2009). Establishment windows used in our study were efficient in overcoming microsite- and propagule-limitation and proved to be effective to introduce characteristic grassland species into the restored species-poor grasslands. Previous studies claimed that at first matrix species should be introduced to the former arable sites (Török et al. 2010, Coiffait-Gombault et al. 2012). This species later can facilitate the establishment of spontaneously immigrated or sown target species. In our study landscape-scale restoration used low-diversity seed mixture after which sown species reached high cover which hamper the establishment of further species. Sown grasses reached high cover scores in only three years after the restoration (Török et al. 2010) and this score decreased slightly six years after the restoration reaching only 65-71% (Kelemen et al. 2014). In this environment we had to create suitable conditions of establishment for our sown target species by violently opening the closed grass sward similarly to other researchers (Pywell et al. 2007, Schmiede et al. 2012, John et al. 2016). After the disturbance and sowing the cover of resident matrix species (*Bromus inermis*, *Festuca pseudovina*, *F. rupicola* and *Poa angustifolia*) in the first two years remained under 10% in all window types and secured available niches and low competition and so facilitated the establishment of sown target species. This findings were in accordance with the findings of by (Zobel et al. 2000, Pywell et al. 2007). The use of the high-diversity seed mixture resulted similar cover scores in alkaline and loess grasslands. These results suggest that using high-diversity seed mixtures one can increase the chance of establishment of different species under different site conditions. We found that similarly to the findings of John et al. (2016) the most crucial period for sown species to establish was the first year. The strong correlation between of the cover and frequency of sown species in the first- and second year also indicated this. Most of the species successfully established in the first year were present also in second year with similar or even increased cover scores. The ability of species to establish and persist in windows suggests that in the future they will get a chance to spread to the restored grassland. Burmeier et al. (2011) observed the ability of species to disperse after 7-8 years to the surrounding grasslands in case of 90% of the introduced species studied by them. We noticed already in the second year the establishment of *Centaurea solstitialis* (a species protected in Hungary) in the surroundings of the establishment windows.

The life history spectra changed from the first year to the second one. Short-lived sown species were more frequent in the first year compared to the second one, when perennials characterised the vegetation. In a vineyard inter-rows high-diversity seed mixtures sowing experiment Miglécz et al. (2015) found similar patterns. In the first year short-lived sown species (*Atriplex litoralis*, *A. tatarica* and *Bupleurum tenuissimum*) were typical. This species are characteristic secondary succession species of alkaline grassland with high stress tolerance (Deák et al. 2015b). The second year's vegetation was mainly characterised by perennial-and loess grassland species (Tóth & Hüse 2014).

Effect of window size

Our results suggest that in restoration projects using larger windows is more appropriate than using smaller ones. Larger establishment windows were characterised by higher cover of sown species and total vegetation cover also had higher scores. DCA ordination also highlighted that the development of larger windows is more stable compared to the smaller ones, where vegetation development was stochastic. This may be the result of their low surface/perimeter ratio, which enables the surrounding vegetation composed by competitive grasses to have greater impact to the development of smaller windows vegetation than is larger ones (Deák et al. 2011).This is in accordance with other studies, where very small windows (window size between 10 cm × 10 cm and 32 cm × 32 cm) were rapidly recolonised by the surrounding vegetation (Ecksteinet al. 2012, Ludewiget al. 2015). So with using larger windows better results can be reached. But establishment windows favours not only sown species but the new niche is also provided for weeds. Soil disturbance in former croplands can support weed species emerging from the soil seed bank resulting in a serious weed infestation (Hutchings & Booth 1996, Bekker et al. 1997, Hölzel & Otte 2003, Török et al. 2012). Our results correspond with the result of Warren et al. (2002). Weeds species establishment in the windows is temporal and small-scale phenomenon, meaning that it does not pose a real threat for restoration. After the sowing of the high-diversity seed mixture the weed cover remained low to moderate (between 18.5 and 30.7%) in the first year. In case of low-diversity seed mixture sowing in ex-arable fields in the same region the weed cover was much higher (64–70%) in the first year after sowing (Török et al. 2012).One likely reason for these differences may be that after the restoration project with low-diversity seed mixtures long-term post-restoration management was applied in the site (mowing, grazing) so the weeds seed bank was not able to reproduce and decreased (Kelemen et al. 2014). Another explanation can be that in the establishment windows we used high-density seed mixture in a rate of 100 kg/ha seed compared to the 25 kg/ha used in low-diversity seed sowing restoration. The high-density of seeds could be more effective in the weed suppression than the low one. Most of the weeds found in our study are only short-lived species, which do not mean a real threat from the restoration ecological viewpoint. The total cover of weed species decreased significantly from the first year to the second one, as found also in the case of two common perennial weeds (*Cirsium arvense* and *Convolvulus arvensis*), in each windows type as a result of the establishment of competitive sown perennial species. This is very important because farmers may be afraid of weed infestation if using larger windows but our results clearly states that weed emergence did not pose real threat when using establishment windows. We recommend the use of 4 m × 4 m sized windows in restoration projects.

Effects of management

The total vegetation cover was lower in grazed than in fenced windows likely because the continuous removal of green biomass by grazing animals (Pavlůet al. 2007, Töröket al. 2014b). In the first two years of the study there were no differences in the total sown species the cover, cover of matrix species and cover of weeds between the managed and unmanaged windows. It seems that management has minor role in early vegetation succession but may have crucial role in long term conservation projects. Without the biomass removal effect of grazing litter can accumulate and microsite availability can decrease in the fenced windows. In long term this may lead tothe disappearance of sown species (Eskelinen& Virtanen2005, Lepšet al. 2007, Kelemenet al. 2014). Grazing animals can also assist in seed dispersal to the remained grassland area (Wesselset al. 2008, Rosenthalet al. 2012, Freundet al. 2014) and also act as a disturbance to the closed sward and create suitable surfaces for further establishment of target species (Eskelinen& Virtanen2005, Mann& Tischew2010, Rosenthalet al. 2012, Freundet al. 2015, Tölgyesiet al. 2015).

Species composition of the grazed large windows was more similar to each other in the second year than that of fenced windows. The lack of management may result stochastic vegetation development and may lead to different results (Moog et al. 2002, Köhler et al. 2005).

In fenced windows vegetation was characterised by short-lived species. In the first year prickly, short-lived species, like *Carthamus lanatus* and *Centaurea solstitialis*, dominated the vegetation, in the second year unprickly short-lived species like *Silene viscosa*, *Trifolium angulatum*, *T. striatum* and *Falcaria vulgaris.* The reason may be that in fenced windows short-lived species have higher chances to set seeds than in grazed ones, so in the next year they can germinate in higher number compared to the grazed windows (Aboling et al. 2008). The effect is just temporary, since the increasing cover of perennial species will increase the competition in the following years.

Conclusions

The disturbance applied in species-poor grasslands closed sward and the use of high-diversity seed mixture in the disturbed patches is a novel approach in restoration. The establishment windows showed to be successful to increase species diversity in species-poor sown grasslands. Windows can be used especially in cases when the chance of establishment of target species by spontaneous succession is low due to the high competition of present grasses and the lack of propagule sources in the surrounding area. The disturbance caused by soil preparation increases new microsites availability and the sowing of high-diversity seed mixtures introduces multiple species propagules to the target area. Our results also suggest the use of larger windows than smaller ones, because they are more effective.

Establishment windows act as biodiversity hotspots, because a high establishment rate of target species was characteristic to the windows. The dispersal ability of this species is still unknown, further studies need to study the dispersal ability of target species to the surrounding area, as well as the persistence of established populations and possible increase of species richness in the whole restored grassland area. Wild boars and rodents are present in the area and can create small-scale disturbance, which is crucial to open the closed sward. Grazing livestock have similar effect and also has role in the dispersal of target species propagules. The use of grazing as management tool is not widely used in the first year after restoration because can cause weed intensification. Our study suggests that establishment windows use can be combined with grazing even in the first year after the creation of windows because grazing had no negative effect in the establishment of target species and did not lead to the encroachment of weeds.

Key results of the dissertation

- In a systematic review we revealed the huge knowledge gap regarding the effect of climate change on the soil seed bank of present plant communities and the ability of the seed bank to buffer the changes.
- The changes of temperature and precipitation regimes will affect the intensity, duration and frequency of disturbances, such as fires and flooding events. The main driver of seed bank changes will be the change in precipitation regimes.
- In our study we revealed that soil seed bank can be a proper source of recovery in wetlands and ecosystems characterised by frequent and unpredictable disturbances. Contrary, in historically stable habitats, active restoration will be needed by propagule introduction.
- In course of restoration projects we suggest to consider the predicted climate changes and to use of native species already adapted to forecasted changes.
- The use of establishment windows in restoration projects is a novel method and we proved that it is efficient to increase microsite availability and to decrease propagule limitation. It can be used efficiently to increase species diversity of species-poor restored grasslands.
- Use of high-diversity seed mixture containing multiple species propagules is efficient to introduce target native species to sites with different conditions.
- Larger establishment windows resulted in stable vegetation development, target species reached highest the cover there.
- Grazing is a proper management tool already in the first year because grazing animals can open new microsites and can disperse target species propagules.

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Összefoglalás

Annak ellenére, hogy a klímaváltozás globálisan fejti ki hatását, a magbankra kifejtett hatása egy ritkán kutatott témakör. Áttekintő tanulmányunkban öt kontinens terültéről találtunk kutatásokat, amelyek direkt vagy indirekt módon köthetőek a klímaváltozás magbankra gyakorolt hatásához, azonban számos régióban további kutatásokra lenne szükség. Kimutattam, hogy a klímaváltozás jelentős, sokszor visszafordíthatatlan változásokat idéz elő a gyepek magbank összetételében. A változások előidézésében a legnagyobb szerepe a csapadékmennyiség változásnak van. A gyepek magbakja jelentős szerephez juthat a változó klimatikus viszonyok között zajló restaurációs folyamatok során. A nedves gyepek, árterek és olyan élőhelyek esetében, ahol a zavarások gyakoriak és periodikusán bekövetkeznek, a perzisztens magbank a megváltozott zavarási rendszerben is képes lehet biztosítani az élőhely regenerációját. A ritkán zavart, történetileg stabilabb élőhelyek magbankjában a tranziens fajok dominálnak, a magbank nem képes pufferelni a megváltozott zavarási rendszerek okozta változásokat. A stabil élőhelyek esetében aktív beavatkozásra van szükség a restauráció során, felhasználva olyan őshonos fajok magvait, amelyek már alkalmazkodtak a megváltozott körülményekhez.

A fajszegény restaurált gyepek fajgazdagságának növelésére használható új módszert mutattam be a dolgozat második felében. Vizsgálatunkban kolonizációs ablakokat használtunk, amihez a zárt gyeptakarót feltörtük és a feltört területre magas-diverzitású magkeveréket szórtunk. A kolonizációs ablakok megnövelték a fajgazdagságot a gyepekben, ugyanis a talaj előkészítésével a restaurált gyepben megszüntettük a mikroélőhely-limitációt, a megkeverék vetésével pedig a propagulum-limitációt. A vetett fajok sikeresen megtelepetek az ablakokban, főleg a nagyobb méretűekben és sikeresnek bizonyultak a gyomfajok visszaszorításában is. A legelést, mint kezelést, már az első évtől alkalmaztuk és ezt továbbra is javasoljuk, mivel a legelő állatok fontos szerepet játszanak új élőhelyek kialakításában és a propagulum terjesztésben.

Új tudományos eredmények

- A klímaváltozás a hőmérséklet és a csapadékmennyiség változásával jár, ami kihat a különféle zavarások időzítésére, erősségére és gyakoriságára is. Eredményeim alapján a csapadékmennyiség változás a magbank változás fő tényezője.
- A magbank bizonyos mértékig képes pufferelni a változásokat, így a természetes zavarásokkal érintett élőhelyeken a restauráció támaszkodhat a magbankra. Ezzel szemben a jelenleg stabil, kevéssé zavart élőhelyeken aktív restaurációs beavatkozásra lesz szükség.
- A restaurációs projekteknél fontos figyelembe venni a klímaváltozást és olyan őshonos fajokat használni, amelyek képesek szembenézni az előrejelzett változásokkal.
- Arról, hogy hogyan hat a klímaváltozás a jelenlegi növényközösségek magbankjára és hogy milyen mértékben képes a magbank pufferelni a klímaváltozás hatására megváltozott körülményeket keveset tudunk. Célzott vizsgálatokra lenne szükség, hogy megértsük a klímaváltozás elsődleges és másodlagos hatásainak jelentőségét a gyepi élőhelyek magbank dinamikájában.
- Kimutattuk, hogy a kolonizációs ablakok sikeresen megszüntetik a mikroélőhely- és propagulum-limitációt, hatékony módszernek bizonyult a fajszegény gyepek restaurálására.
- A magas diverzitású magkeverékek hatékonyan alkalmazhatóak fajgazdagság növelésére különböző tulajdonságú területeken.
- A legnagyobb méretű kolonizációs ablakokban érték el a célfajok a legnagyobb borítási értékeket valamint ezekben volt a legstabilabb a vegetációfejlődés. A restaurációs projektekben tehát javasolt a nagyobb méretű ablakok használata.
- A legelés már az első évtől alkalmazható kezelési módszer, a legelő állatok alkalmasak új mikroélőhelyeket létrehozására és a célfajok terjesztésére.

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