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Local topography affects seed bank successional patterns in alluvial meadows

Alena Havrdová*, Jan Douda, Jana Doudová

Faculty of Environmental Sciences, Czech University of Life Sciences Prague, Kamýcká 129, Praha 6–Suchdol, CZ-165 21, Czech Republic

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ABSTRACT

Seed banks may play a crucial role in the maintenance of community diversity, but their role on semi-natural grasslands, one of the most species rich habitats in Europe, is usually unexplored in population and community studies. We aim to clarify how local factors and topography influence seed bank successional patterns on semi-natural alluvial meadows. All 35 meadows were situated in the Eagle (Orlické) Mountains in the Czech Republic and were divided according to fallow time. Paired plots, represented low and high topography, were established on each meadow. We recorded plant species occurrence in vegetation and in the seed bank to ascertain how seed abundance, diversity and the similarity between seed bank and vegetation were influenced by topography and management. Seed abundance significantly changed, whereas seed diversity remained stable after meadow abandonment. Seed abundance was high in the low topography plots probably due to higher aboveground biomass which promoted seed accumulation. In the high topography plots, seed abundance was low in managed meadows, but seeds were accumulated after abandonment. Similarity between the seed bank and vegetation was low, but over half of the typical meadow species survived in the seed bank for long periods of time, even when they had disappeared from the aboveground vegetation. In conclusion, the local topography of alluvial meadows influenced seed bank successional patterns, mainly seed abundance, similarity between the seed bank and vegetation and responses of individual species in the seed bank. Seed bank successional patterns are dependent on specific habitat conditions and communities with high seed bank accumulation are more stable and better restored than communities where the seed bank has become severely depleted.

1. Introduction

The European landscape has significantly changed over the last few decades and a cessation of traditional management practises is one of the most important causes of this change. Many semi-natural grasslands, which are one of the most species rich habitats in Europe (Kull and Zobel, 1991; Lepš, 2005), have been undergoing spontaneous succession and their high plant diversity is in danger (Diemer et al., 2001; Falińska, 1991; Losvik, 1999; Poschlod et al., 2005). It seems that seed banks play a crucial role in the maintenance of community diversity over the longer term because they are important reserves of viable seeds (Baskin and Baskin, 2001; Chambers and MacMahon, 1994; Leck et al., 1989).

Unfortunately, there has been very little research into the role of seed banks in population and community structures and this can lead to incorrect survival predictions for individual species, underestimation of diversity and false conclusions about coexistence mechanisms in plant communities. It is still unclear as to whether the seed bank has any role in the restoration of degraded meadows. Recently, a few studies have shown that the seed bank serves as a reserve for species, even after a relatively long period of time (Auffret and Cousins, 2011; Erfanzadeh et al., 2013; Kalamees et al., 2012; Valkó et al., 2011). However, many studies have found that most of the key and characteristic species of semi-natural grasslands only accumulate transient seed banks (Bekker et al., 1997; Jensen, 1998; Kalamees and Zobel, 1998; Milberg, 1992; Mitlacher et al., 2002; Rosef, 2008).

Vegetation is highly influenced by species specific processes, such as habitat filtering and species interactions (Douda et al., 2012; Lepš, 2005), but seed diversity and seed abundance depend on composition of recent and past seed rain events (Jensen, 1998; Kettenring et al., 2006), seed dormancy (Thompson et al., 1997) and local factors that affect the balance between seed accumulation and seed depletion (Leck et al., 1989; Schafer and Chilcote, 1969). The storage of viable seeds in the soil is primarily conditioned by

* Corresponding author.
E-mail addresses: havrdovaa@fzp.czu.cz (A. Havrdová), douda@fzp.czu.cz (J. Douda), janadoudova1@gmail.com (J. Doudová).

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seed dormancy (Thompson et al., 1997), but the accumulation and depletion of seeds are also driven by local factors that influence germination and seed decay, such as light penetration to the soil surface (Silvertown, 1980; Xiong and Nilsson, 1997), water regime (Bekker et al., 1998; Dos Santos et al., 2013; Gomaa, 2014; Hill and Vander Kloet, 2005), animal activities (Edwards and Crawley, 1999; Milton et al., 1997) and management practices (Kalamees and Zobel, 1998).

Succession has been found to be an important driver affecting seed bank composition in semi-natural grasslands and previous studies have suggested several alternative scenarios about changes in seed bank abundance and diversity during succession, i.e., several different seed bank successional patterns (Bossuyt et al., 2006; Falińska, 1999; Jacquemyn et al., 2011; Milberg, 1995). Differences in successional patterns can be caused by climate, landscape differences (i.e., the regional species pool, Bekker et al., 1997) and specific local environmental conditions. It has been suggested that in managed wet meadows, seed abundance is often reduced because biomass removal accelerates seed germination and because the seeds are carried away when the hay is removed. Therefore, as early as 5 years after abandonment, seed abundance has been shown to increase due to high seed input and lack of light for germination (Falińska, 1999). Alternatively, on calcareous grasslands seed diversity and abundance after abandonment remained stable, even after shrub formation, i.e., 20–50 years after abandonment (Bakker et al., 1996; Bossuyt et al., 2006; Kalamees and Zobel, 1998) or seed abundance started to decline after the land had been abandoned for just 10 years, even though the decrease in seed diversity was negligible (Jacquemyn et al., 2011; Kalamees et al., 2012). In the later stages of succession, the situation was more or less the same for all types of meadows, specifically both the number of seeds and species diversity declined. This decline was caused by processes that lead to seed bank depletion together with the limited seed supply from vegetation in the late succession stage when species often reproduced vegetatively (Falińska, 1999).

We chose local topography as a factor that could strongly control productivity in alluvial meadows in order to clarify the importance of local factors that may cause differences in seed bank successional patterns. Previous studies suggested that increased biomass and vegetation cover on the more productive sites would reduce germination from the seed bank and inhibit seed depletion of grassland species (Silvertown, 1980; Xiong and Nilsson, 1997). Therefore, we hypothesised that changes in the seed bank during succession would be less apparent on more productive low topography meadow parts than on less productive high topography meadow parts where the seed bank should deplete more rapidly. Furthermore, we assumed that the ability to predict seed bank composition from vegetation would be greater in sites where seed accumulation predominates, i.e., after abandonment and in low topography areas. However, the seed bank after abandonment in both topographic areas can reflect past rather than present vegetation composition and some meadow species absent in vegetation can persist in seed bank and serve as source for restoration. Generally, we expected that the proportion of meadow species in a seed bank over the course of succession would fall, but the rate of decline could be affected by environmental variables linked to topography.

In this study, we focused on how local factors influenced seed bank successional patterns. We addressed the following specific questions: (1) How do seed bank abundance and diversity differ between managed and unmanaged meadows in relation to topography? (2) Is it possible to predict seed bank composition from current vegetation or does seed bank composition reflect past vegetation? (3) Can characteristic meadow species persist for long periods of time in seed banks after abandonment and is this survival influenced by topography?

2. Material and methods

2.1. Study area and sampling design

All the study meadows were located in the Eagle (Orlické) Mountains (16°18′–16°36′E, 50°07′–50°23′N; Fig. 1) in the northeastern part of the Czech Republic. The Eagle Mountains cover 204 km^2 and range from 416 to 1115 m a.s.l. They are made up of a mountain range and deep valleys with a rich network of streams that are often bordered by alluvial meadows. Establishment of these semi-natural meadows was connected to human settlement, which flourished at the end of the 19th and the beginning of the 20th century. They started to be abandoned in the 1940s when the Sudeten Germans were expelled, but most of them have been unmanaged for less than 20 years. Those that are still managed are mown once per season and some are also extensively grazed. Mean temperatures range from −3.7 °C in January to 16.0 °C in July and mean annual precipitation is 928 mm. The area is predominantly geologically made up of metamorphic rocks and arenaceous marl sediments.

The study sites in the alluvial meadows were selected using several procedures. At first, we used hydrological maps in ArcGIS 9.3 (Ormsby et al., 2008) to divide all the water streams into 500 m segments and then identified the segments that were surrounded by non-forest habitats (120 segments in total). The segments that were surrounded by managed and unmanaged meadows (no fertilization, ploughing, drainage and/or recent graz-

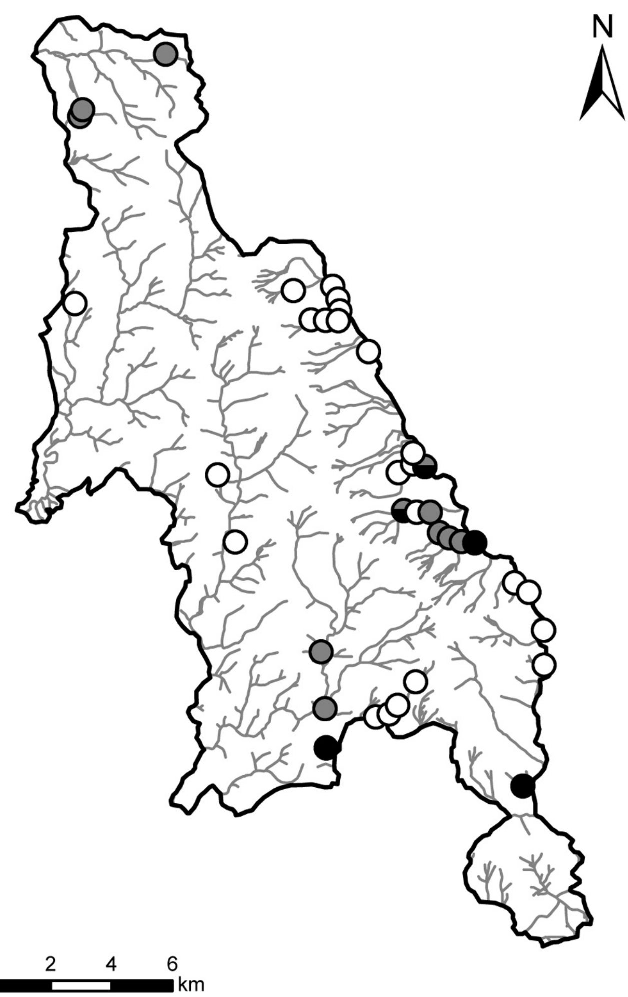

Fig. 1. The 35 studied meadows bordering water streams in the Eagle Mountains. White circles: regularly managed meadows (M), grey circles: meadows unmanaged for <40 years ($UM_{<40}$) and black circles: meadows unmanaged for >40 years ($UM_{>40}$).