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Low seed pressure and competition from resident vegetation restricts dry grassland specialists to edges of abandoned fields

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ABSTRACT

The occurrence of 66 dry-grassland species was compared between the edges and the interiors of 48 abandoned fields in northern Bohemia, Czech Republic, Europe. More species occurred at the edges than in the interiors. The proximity of the source grassland had a positive effect on species richness at the edges but not in the interiors. Soil characteristics did not differ between the edges and the interiors, but aboveground biomass was significantly lower at the edges, suggesting that edges have more open vegetation and provide more microsites suitable for colonisation.

Neither dispersal traits nor habitat requirements were significantly associated with species that were more narrowly restricted to the edges of fields. However, the species that occurred more often at the edges than in the interiors were those that were infrequent in dry grasslands within the study area. These species responded positively to the grassland neighbourhood, they had a narrower niche, lower specific leaf area, a shorter persistence in the seed bank and a later initiation of flowering. The results of the study indicate that low microsite availability, together with low seed pressure, is most limiting for these specialised and competitively inferior species. For this reason, they are much more restricted to dry grasslands, and their conservation relies primarily on proper management of their current habitats. The suitability of abandoned fields for grassland specialists could be enhanced by disturbance that would create colonisation microsites, and successful recruitment of grassland species can be supported by seed additions.

1. Introduction

Abandoned fields provide an interesting study system for testing ecological theories. Additionally, they represent an important challenge for the practice of ecological restoration (Cramer et al., 2008). Fields in regions with a drier climate and nutrient-poor or shallow soils remain open and almost treeless during long periods after abandonment (Osbornová et al., 1990; Jongepierová et al., 2004; Ruprecht, 2006). Therefore, abandoned fields can be viewed as potential habitats for species from grasslands (Walker et al., 2004,b; Öster et al., 2009a,b; Knappová et al., 2012). Grasslands are among the valuable and species-rich habitats that are threatened by ongoing land use changes (Münzbergová, 2004; Pärtel et al., 2005; Chýlová and Münzbergová, 2008). The species richness of grasslands relies to a large extent on a suitable management regime, usually mowing or grazing, that prevents more competitive species from achieving dominance (Pärtel et al., 2005). Under certain circumstances, e.g., if the seed source of the target species is nearby and the seed bank of the ruderal species is missing, field succession might lead to grasslands of high conservation value with only minimum human intervention or with no human intervention at all (Jongepierová et al., 2004; Ruprecht, 2006). In most cases, however, the colonisation of abandoned fields by desirable (e.g., grassland) species is constrained by both habitat conditions and seed availability (Buisson et al., 2006; Öster et al., 2009b; Knappová et al., 2012), and successful succession towards a grassland requires regular management or the assisted transfer of plant material (Pywell et al., 2002). The aim of this study was to explore whether abandoned fields in northern Bohemia, Czech Republic, central Europe can be considered suitable habitats for dry grassland plant species and to identify the main limiting factors for the successful spontaneous colonisation of these fields.

Habitat suitability can be most directly assessed by seed addition experiments (Münzbergová and Herben, 2005; Öster et al., 2009b), but they are hardly applicable routinely on a large scale due to their high time and work demands. Moreover, the results can be strongly dependent on the amount of seeds added

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(Münzbergová, 2012) and sensitive to differences in habitat requirements between seedlings and adult plants (Ehrlén et al., 2006; Knappová et al., 2013).

An alternative approach to gain insights into different types of limitation is to collect indirect evidence by comparing the edges and interiors of the sites under consideration (Buisson et al., 2006). Assuming that edges and interiors exhibit similar environmental characteristics they should have the same species richness and species composition in the case of unconstrained colonisation. Possible differences in the characteristics of species prevailing at the edges compared to the species in the field interiors could provide important insights into the factors limiting colonisation. In particular, differences in *habitat requirements* between species occupying edges and interiors could suggest that the conditions found in the fields actually do not meet the habitat requirements of species occurring predominantly at the edges and that the populations of these species in the fields function as sinks that are maintained only by seed input from the nearby sources. Differences in *dispersal traits* between species prevailing at the edges and species that are also common in the field interiors would suggest that for species with poor dispersal, the time since abandonment was not long enough to overcome a distance of a few meters from the edge to the interior. Alternatively, abandoned fields could be rather unsuitable (i.e., a sink) habitat for grassland species; in this case, the populations of the grassland species in the abandoned fields would be maintained by the seed supply from nearby sources.

The fields investigated in this study were abandoned approximately 20 years ago. This time interval should be sufficiently long for species to not only reach the closest field edge but also (given that abandoned fields represent suitable habitats) spread further into the interior of the field. This does not mean, however, that the abandoned field would resemble the grassland 20 years after abandonment. The traces of former cultivation can be apparent decades or even centuries after abandonment (Romermann et al., 2005). Nonetheless, most species of the target grassland community are usually already present after 10–20 years of succession (Osbornová et al., 1990; Willems, 2001; Ruprecht, 2005), although succession towards grassland can sometimes be inhibited for a long period by vigorously growing weeds (Willems, 2001; Cramer et al., 2008).

To identify the factors that most influence the colonisation of abandoned fields, we aimed to answer the following questions:

1) How do the species richness and species composition of grassland plants differ between the edges and the interiors of abandoned fields?
2) How does the species richness of grassland plants in field interiors depend on richness at field edges?
3) What is the importance of the presence of neighbouring source grasslands for the species richness and species composition of grassland plants in the abandoned fields?
4) Can differences in the affinity of species to the edges of abandoned fields and in the response of species to the grassland neighbourhood be explained by any differences in the characteristics of the species?

2. Methods

2.1. Study region and target species

This study was performed in the northern part of the Czech Republic in an area delimited by the towns of Litoměřice, Úštěk and

Table 1
List of 66 target dry grassland species occurring in 48 surveyed abandoned fields and number of their occurrences in edge and interior. Numbers in brackets denote the number of fields in which individual species occurred solely at the edge or in the interior. Species shown in bold were found solely at the edges. Nomenclature follows Tutin et al. (1964–1980).

Species	Number of occurrences		Species	Number of occurrences	
	Edges	Interiors		Edges	Interiors
Agrimonia eupatoria	46 (8)	39 (1)	*Knautia arvensis*	35 (17)	19 (1)
Anthyllis vulneraria	1 (0)	1 (0)	*Koeleria macrantha*	4 (3)	1 (0)
Artemisia campestris	2 (0)	2 (0)	***Laserpitium latifolium***	1 (1)	0 (0)
Asperula cynanchica	3 (2)	1 (0)	*Leontodon hispidus*	6 (4)	2 (0)
Aster amellus	4 (2)	2 (0)	*Linum catharticum*	18 (9)	12 (3)
Astragalus cicer	21 (8)	15 (2)	*Linum flavum*	1 (0)	1 (0)
Astragalus glycyphyllos	32 (3)	32 (3)	*Lotus corniculatus*	28 (13)	17 (2)
Brachypodium pinnatum	28 (12)	16 (0)	*Medicago falcata*	2 (2)	2 (2)
Briza media	4 (3)	1 (0)	*Melampyrum arvense*	4 (3)	1 (0)
Bromus erectus	10 (5)	7 (2)	*Melampyrum nemorosum*	1 (0)	1 (0)
Bupleurum falcatum	30 (15)	20 (5)	***Onobrychis viciifolia***	6 (6)	0 (0)
Carex flacca	2 (2)	0 (0)	*Ononis spinosa*	2 (1)	1 (0)
Carex humilis	1 (1)	0 (0)	*Origanum vulgare*	34 (6)	30 (2)
Carex tomentosa	1 (1)	1 (1)	*Peucedanum cervaria*	4 (3)	1 (0)
Carlina vulgaris	16 (5)	11 (0)	*Pimpinella saxifraga*	6 (2)	5 (1)
Centaurea jacea	31 (12)	22 (3)	*Plantago media*	13 (5)	13 (5)
Centaurea rhenana	2 (1)	1 (0)	***Potentilla arenaria***	1 (1)	0 (0)
Centaurea scabiosa	24 (16)	9 (1)	***Potentilla heptaphylla***	4 (4)	0 (0)
Cirsium acaule	2 (2)	0 (0)	*Primula veris*	5 (4)	1 (0)
Cirsium eriophorum	9 (4)	7 (2)	*Prunella grandiflora*	3 (3)	1 (1)
Coronilla varia	42 (8)	37 (3)	***Salvia nemorosa***	4 (4)	0 (0)
Dianthus carthusianorum	1 (1)	2 (2)	*Salvia pratensis*	4 (2)	2 (0)
Eryngium campestre	9 (8)	3 (2)	*Salvia verticillata*	29 (11)	19 (1)
Euphorbia cyparissias	35 (20)	15 (0)	*Sanguisorba minor*	15 (12)	5 (2)
Euphrasia rostkoviana	4 (4)	2 (2)	*Scabiosa ochroleuca*	23 (10)	14 (1)
Festuca rupicola	37 (16)	22 (1)	*Scorzonera hispanica*	1 (0)	1 (0)
Fragaria viridis	37 (10)	29 (2)	*Stachys recta*	18 (12)	8 (2)
Galium verum	26 (9)	19 (2)	*Tanacetum corymbosum*	4 (3)	1 (0)
Gentiana cruciata	7 (2)	6 (1)	***Thymus praecox***	2 (2)	0 (0)
Genista tinctoria	4 (2)	2 (0)	*Tragopogon pratensis*	4 (1)	3 (0)
Hieracium pilosella	9 (6)	4 (1)	*Trifolium medium*	23 (13)	11 (1)
Inula hirta	3 (3)	0 (0)	***Trifolium montanum***	1 (1)	0 (0)
Inula salicina	37 (8)	29 (0)	*Veronica teucrium*	3 (2)	1 (0)