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Soil seed bank in managed and abandoned semi-natural meadows in Soomaa National Park, Estonia

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The seed bank of four sites representing different stages of semi-natural meadow succession in a west Estonian floodplain was investigated using the seedling emergence method. For 40 species, seed bank persistence types could be determined. Most grassland species were found to have a short-term persistent or a transient seed bank. Sites where management had ceased were found to have a significantly higher number of seeds of *Carex* spp., and, at least at the long-term abandoned site, a significantly lower number of seeds of grassland herbs. The highest number of grass seeds was found at the managed site, although this was non-significant. Similarity between seed bank and vegetation decreased with increasing time since abandonment and with soil depth. Implications for restoration are discussed. This study confirms that only on recently abandoned sites can the seed bank play a significant role in meadow restoration.

Key words: ecology, restoration management, seed bank persistence, semi-natural meadows

Introduction

From the 19th century onwards, but most markedly in the last 50 years, agricultural development has led to an enormous loss of semi-natural grassland in large parts of Europe (van Dijk 1991, Joyce & Wade 1998). In northern Europe, this loss has, for example, been documented for Sweden (Linusson *et al*. 1998) and Finland (Marttila *et al*. 1999 and references therein). In Estonia, where the present study was carried out, a large fraction of semi-natural grassland was converted to intensive grassland from 1950 onwards. Mowing by hand was replaced by mechanized mowing (Truus & Tõnisson 1998). To increase agricultural productivity, artificial fertilizer and livestock manure were used on a large scale, and many grasslands were re-seeded, using hay species such as *Alopecurus pratensis* and *Dactylis glomerata* (Pork 1979, Ehrlich 1996, Truus & Tõnisson 1998). Nevertheless, a large fraction of those meadows situated in floodplains escaped agricultural conversion, compared to elsewhere in Europe. Palo (1996a) estimated that floodplain meadows with high nature conservation value still covered an area of ca. 12 500 ha in Estonia. However, many semi-natural floodplain meadows were abandoned as a consequence of the political change in 1991, when the country regained its independence. As a consequence, large areas of semi-natural meadows are now gradually being replaced by species-poor successional tall herb communities and willow scrub (Palo 1996b). The problems arising from a lack of management of semi-natural grassland and the resulting vegetational changes have been described by various authors (e.g. Jukola-Sulonen 1983, Hæggström 1988, Londo 1990, Huhta 1996). For the restoration of such grasslands it is important to know which of the species disappearing from the vegetation in the course of succession build up a long-term or at least a short-term persistent seed bank in the soil. Though much is known about the seed bank ecology of species of fertile grasslands, only a few studies so far have investigated the seed bank of managed semi-natural wet meadows (Pfadenhauer & Maas 1987, Milberg 1992, 1993, Maas & Schopp-Guth 1995), and even fewer focused on abandoned stages of these grasslands (Milberg 1995, Jensen 1998, Falinska 1999). Therefore, "almost nothing" is known about the seed bank ecology of species primarily occurring in these less productive semi-natural grasslands (Thompson *et al*. 1997: 21).

The present study investigates the composition and vertical distribution of soil seed banks on sites ranging from currently managed to long-term abandoned and interprets the results from a restoration point of view.

Methods

Site description

The study was carried out on floodplain meadows on the east side of the river Halliste near the centre of Soomaa National Park (58°25´N, 25°02´E), in western Estonia. The climate in the study area is transitional between a maritime climate and a continental climate. Mean annual precipitation is 600 to 650 mm, with a maximum monthly rainfall of about 85 mm falling in July and August. The mean annual air temperature in the region is 4.5 to 5.0 °C, ranging between –6.5 °C in February and 17 °C in July (Laasimer *et al*. 1993, Kink 1996). The area is characterized by regular spring flooding and occasional autumn flooding (Peterson 1994), with the flood duration being rather long, due to the even topography in this region (Masing *et al*. 2000). The dominant soil types in the study area are Fluvisols, Gleysols and, in some areas, Eutric Histosols and Humic Gleysols (Eesti Põllumajandusprojekt 1980). Traditionally, most meadows in the area were used as wooded meadows (i.e. haymaking in summer and as a common practice aftermath grazing). From the 1950s up until 1991 the meadows were managed by kolkhozes, with a management regime very similar to the traditional management, the only differences being cessation of aftermath grazing and mowing by tractor instead of cutting by scythe. In exceptionally wet years the meadows were not mown. Since 1991 the meadows have been abandoned.

Early successional stages in the area are dominated by the tall herb *Filipendula ulmaria* and the sedges *Carex cespitosa* and *C. disticha*. Later stages are characterized by willow scrub, with *Salix cinerea*, *S. pentandra* and *S. triandra* being the most common species.

Four sites representing distinct stages of secondary succession were investigated: two in the Tõramaa area, and two at 1.5 km distance in the Piiri area. The sites were chosen to represent stages ranging from currently managed to long-term abandoned. Consequently, these sites are referred to by the abbreviations T0, P4, T8 and P25, where the letters T and P denote the two areas and the number refers to years since abandonment. Time since abandonment for the sites P4 and P25 was estimated using year ring counts for the largest willows at each site, as no direct information could be gained on the land-use history of these abandoned sites.

Sampling methods

On each site a representative 15 m × 15 m plot was marked out with pegs in May 1998. Viable seed bank and vegetation were sampled within these plots, as detailed below. Seed bank samples were taken between 25 and 27 May 1998, before seed dispersal had begun. On each site ten randomly located subplots of 1 m × 1 m were sampled using a soil corer with a diameter of 4 cm. In each subplot, ten soil cores were extracted on a regular grid (one central row of four cores and two outer rows of three cores each). After removal of the litter layer, the cores were divided into segments of 0–2 cm, 2–6 cm and 6–12 cm, based on Thompson *et al.*'s (1997) recommendation of sampling at least two different layers. The shallow surface layer of 0–2 cm was included in the sampling design because, given the inability of many species to emerge from greater depths (Harper 1977), this better reflects the potential of regeneration from seeds in the absence of soil disturbance than the commonly employed sampling of a 0–5 cm surface layer. This design is compatible with Thompson's (1993) key of seed bank classification, which uses the vertical distribution of seeds for the determination of the persistence type.

The ten segments for each depth were pooled. This produced a total sample area of ca. 1257 cm^2 for each site, and a respective volume of 15.1 litres. This is well above the recommendations given by Hutchings (1986), who recommended 1.0 to 1.2 litres of soil for grassland communities and eight to twelve litres for climax forest.

The pooled soil samples were concentrated using the bulk reduction method, which is an adequate method for short-term seed bank studies, as this method promotes rapid and complete germination of the seeds of many species (ter Heerdt *et al.* 1996). The soil was washed through two sieves of 2.0 mm and 0.2 mm, respectively. By doing so, rhizomes and roots were eliminated from the samples, and the removal of coarse and very fine soil particles resulted in considerable bulk reduction. Due to technical problems, however, only five samples of T8 could be processed.

The samples were spread in separate trays into layers with a thickness of ca. 5 mm, overlying a layer of heat-sterilized sand/peat mixture with a thickness of 3 cm. On 3 June 1998 the samples were placed on a table outdoors, allowing natural daily temperature fluctuations to promote germination (*see* Thompson & Grime 1983, Poschlod 1991). The samples were covered with a fine gauze material, which allowed free gas and moisture exchange, but prevented contamination by wind-borne seeds. The effectiveness of the gauze was assessed by monitoring ten control trays containing sand/peat mixture only. The trays were watered regularly, and checked for seedlings on a weekly basis. Seedlings were identified using the key of Muller (1978) and then extracted. If a seedling was not identifiable, it was transplanted into a flower-pot and grown until identification was possible. Identification to the species level was not always possible and in these cases seedlings were pooled. Consequently, *Ranunculus acris* was pooled with *R. repens*, *Stellaria graminea* with *S. palustris*, and all *Carex* spp. with each other except *C. pallescens* and *C. panicea* (the nomenclature follows Tutin *et al.* 1964–1980).

After the beginning of September no new seedlings emerged and, after 15 weeks, the experiment was terminated on 19 September 1998. Although some viable seeds may have remained in the soil samples beyond the experiment, the application of the concentration method — for reasons discussed by ter Heerdt *et al.* (1996) — should have resulted in complete germination of seeds of most species within the first 6 weeks.

The vegetation was sampled in early July. In each plot 25 quadrats of 2 m × 2 m were laid out in a regular grid of 5 × 5 quadrats, the quadrats separated from each other by an interspace of 1 m width. Cover estimates were taken using the decimal cover scale of Londo (1976).

Data analysis and seed bank classification

One-factorial analysis of variance was performed to compare the four sites, testing for differences in (a) the mean number of species in the vegetation per quadrat, (b) the mean number of seed bank species per pooled soil sample and (c) the mean total number of seeds per pooled soil sample.

Juncus spp. and ruderal species (the latter defined as typical species of disturbed habitats according to Ellenberg 1992) occurred irregularly and were excluded, and tests (b)

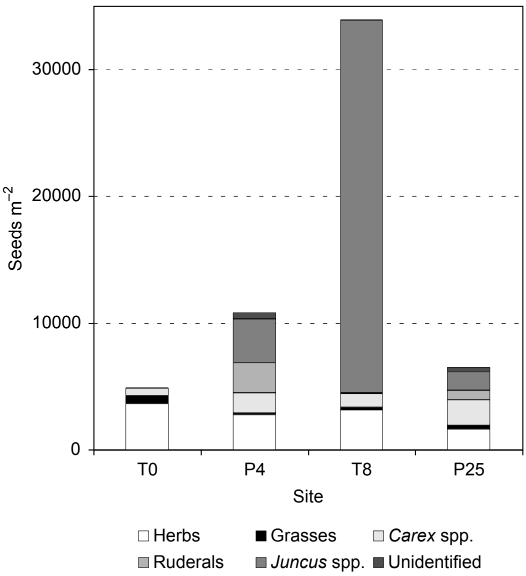

Fig. 1. Seed bank composition of the investigated sites. The displayed seed densities are based on seedling emergence data for herbs, grasses, *Carex* spp., ruderal species (others than *Juncus* spp.), *Juncus* spp., and unidentified seedlings.

and (c) were repeated for the grassland seed bank *sensu stricto*. This was considered to be more meaningful for assessing the potential of the seed bank for contributing to the restoration of wet grassland vegetation. Additional comparisons were also made for mean numbers of seeds of the three pooled groups: *Carex* spp.; grasses; grassland herbs (excluding ruderals). The numbers of seeds were log-transformed prior to analysis to fulfil the assumption of normally distributed data required for ANOVA. A Levene test for homogeneity of variances (*see* Underwood 1997) showed that sample variances differed significantly. For this reason, a Games-Howell post-hoc test was chosen for mean value comparisons (Sokal & Rohlf 1995).

The vertical distribution of seeds of individual species in the soil was also analysed. This distribution, together with a species presence or absence in the vegetation provides the basis for seed bank classification (Thompson 1993). The non-parametric Friedman test for matched samples was employed to test for the occurrence of significant differences within the sampled soil profile, since, as expected (e.g. Thompson 1986), seed density per unit volume for individual species varied much between samples and normal distribution of the data could not be achieved by data transformation. In the case of significance, Wilcoxon Signed Ranks tests for matched samples were employed to indicate which pair(s) of depths differed significantly.

The seed bank type of the species found in the seed bank was determined using the key proposed by Thompson (1993) in a slightly modified form. Departing from this key, species which were found in the vegetation but not in the seed bank (*see* Appendix 2) were not classified as transient. This is because the absence of seedlings of these species does not necessarily prove the absence of seeds (*see* Discussion).

To examine the similarity between vegetation and seed bank, based on the relative frequencies (ranging from zero to one) of 102 species occurring in the seed bank and/or vegetation (pooled species were excluded), reverse phi-square values were calculated (SPSS Inc. 1991). These are standardised, unlike the chi-square measure they are derived from, their values ranging between 0 and 1, with higher values indicating a greater similarity between two samples. The calculation was done for both separate strata and the pooled profile. In this way, similarity with the vegetation could also be investigated individually for all three sampled soil strata.

Results

Seed bank composition

A total of 4927 seedlings emerged from the soil samples, of which 4789 could be identified and assigned to 53 different taxa (50 species and the three above mentioned aggregates). This excludes seedlings of *Betula pubescens* and *Taraxacum officinale* agg. which were dispersing at the same time as the soil samples were being processed. The only contaminant found among the control trays was a single seedling of *Cerastium fontanum*, and this was considered adequate proof of the effectiveness of the gauze in excluding external seed propagules.

Figure 1 displays overall seed densities found at the investigated sites, partitioned for the following species groups: grasses; *Carex* spp.; *Juncus* spp.; herbaceous ruderals (= ruderals); grassland herbs (= herbs). The distinction between herbaceous ruderals and grassland herbs is based on the primary habitat of the species according to Ellenberg (1992). The graph demonstrates clearly, that the number of seedlings of ruderals and of *Juncus* species varies enormously between sites with no clear links between site age and seed bank density.

Overall species total for vegetation and seed bank samples show a generally declining pattern with time of abandonment (Table 1). This decline is more pronounced for the established vegetation than for the seed bank. The pattern is more obvious when only grassland species are considered.

Average density of species in the vegetation per 4 m^2 quadrat was more than 50 % lower at sites that were abandoned for more than four years (Table 1).

In mean number of species per pooled seed bank sample, the recently abandoned site P4 is more diverse than either the currently managed or longest abandoned sites (Table 1). The pattern alters when only grassland species are considered. In this case, the mean numbers of species are greater at the sites of no or four years abandonment than at the site (only one site of 25 yrs. was investigated) of 25 years abandonment (Table 1).

Patterns for seed density per m^2 are similar to those for species per pooled sample. Overall seed density at the currently managed site was two to seven times lower than at the mid-term fallows (P4 and T8 respectively), and did not significantly differ from the longest abandoned site. Again, when considering only grassland species, the pattern changes somewhat, as total densities do not differ across all sites (Table 1).

Comparison of more detailed taxonomic groupings (*see* Table 1) reveals that seed densities of *Carex* spp. at the longest abandoned site are over three times higher than, and herb species less than half of, those at the currently managed site. Seed density of grasses spp. was at least twice as high at the managed site compared to the other sites, but differences were not significant. A detailed overview of the emerged seedlings for the four investigated sites is given in Appendix 1. Appendix 2 lists the species which were found in the established vegetation at least at one site but not recorded as seedlings.

Table 1. Seed bank density and number of species in the vegetation and seed bank of the investigated sites. Total numbers and mean values ± standard deviation for 25 quadrats respectively 10 pooled soil samples (site T8: 5 pooled soil samples) are given. One-way ANOVA *p*-values indicate significant differences in means between sites. Superscripts indicate the identity of means that significantly differ from each other ($p < 0.05$), as given by a post-hoc Games-Howell test.

		Site			
	p	T0	P4	T8	P25
Vegetation					
Species total		63	67	37	32
Species density/4 m^2	< 0.001	26.1^a ± 5.1	25.5^a ± 3.9	12.2^b ± 3.6	9.4^c ± 2.4
Seed bank					
Species total		27	27	25	23
Species density/soil sample	< 0.001	12.4^b ± 4.3	17.4^a ± 2.3	14.0^{ab} ± 3.4	10.0^b ± 2.5
Number of seeds/m^2	< 0.001	4902^b ± 2666	10815^a ± 2387	33948^a ± 24558	6517^b ± 3270
Seed bank of grassland species only (excludes *Juncus* spp. and ruderal species)					
Species total		26	19	21	18
Species density/soil sample	0.015	12.3^a ± 4.5	11.0^a ± 2.4	11.4^{ab} ± 3.0	7.6^b ± 2.2
Number of seeds/m^2	0.871	4878 ± 2682	4472 ± 1454	4440 ± 1677	3947 ± 1800
Seeds of *Carex* spp./m^2	< 0.001	605^c ± 460	1576^{ab} ± 688	1082^{bc} ± 336	2037^a ± 961
Seeds of Poaceae spp./m^2	0.134	637 ± 640	143 ± 190	191 ± 107	286 ± 340
Seeds of herb species/m^2	0.010	3637^a ± 1782	2753^{ab} ± 1125	3167^{ab} ± 1501	1623^b ± 784

Vertical profile

Table 2 lists the species which showed a significantly heterogeneous depth distribution over the sampled profile on any of the sites. Due to the reduced sample size for the seed bank of site T8, no significant results were obtained for this site. At the other sites, patterns of heterogeneity appeared to be linked with overlying vegetative cover. All species with a significantly higher seed density near the soil surface were also present in the vegetation at that site. Species of which seed density peaked at intermediate soil depths (2–6 cm) were scarce or absent from the vegetation, while species with higher seed densities in the lower soil layer were all absent from the overlying vegetation.

Figure 2 displays the percent fractions of grassland herbs, grasses, sedges (*Carex* spp.) and unidentified seedlings for the different depths sampled at the four sites. The only site with a notable fraction of grass seeds in the different layers is the managed meadow site T0. Between 70% and 80% of the seed bank at the meadow site T0 is represented by grassland herbs, and this is relatively constant across the sampled profile. Conversely, in the long-term abandoned site P25 ca. two thirds of the seeds found in the surface layer are of *Carex* species.

Comparison between seed bank and vegetation

The calculated reverse phi-square coefficients (Table 3) show decreasing similarity between the seed bank and overlying vegetation with both increasing soil depth (rows) and increasing duration of fallow (columns). Site T8 presents a slight anomaly in this pattern, probably partly due to greater variance as only five of the ten samples could be used in the analysis (*see* Methods).

Discussion

Seed bank composition

The higher seed density at mid-term fallow stages compared to currently managed and long-term abandoned stages is in good agreement with results of other studies on abandoned wet grasslands (Jensen 1998, Falinska 1999). In the long-term study by Falinska (1999) on an abandoned wet meadow in Białowieża National Park in Poland, seed bank density peaked between five and fifteen years after abandonment, followed by a decrease. Jensen's (1998) study — investigating North German wet meadow sites with abandonment ranging from one year to fifteen years

Table 2. Occurrences of significantly heterogeneous vertical distribution in the soil seed bank. Taxon name followed by Friedman test significance level (* = $p < 0.05$; ** = $p < 0.01$, *** = $p < 0.001$). Percent cover in the vegetation (average of 25 quadrats; – for absence from vegetation) in brackets. Species aggregates are not included.

Site	Higher density near surface	Higher density at intermediate depth	Higher density at greater depth
T0	*Deschampsia cespitosa* * (6.1)		*Stachys palustris* * (< 0.1)
	Leontodon autumnalis * (0.1)		
	Veronica longifolia * (0.5)		
P4	*Carex panicea* ** (31.9)	*Carex pallescens* ** (0.2)	*Gnaphalium uliginosum* * (–)
	Luzula campestris ** (0.1)	*Galium uliginosum* ** (0.1)	*Juncus articulatus* * (–)
	Viola canina ** (0.2)	*Ranunculus auricomus* ** (0.1)	*Plantago intermedia* * (–)
		*Juncus bufonius** (–)	*Polygonum arenastrum* * (–)
			Rorippa islandica *** (–)
P25		*Agrostis gigantea* ** (–)	
		Veronica scutellata *** (–)	
		Viola canina * (–)	

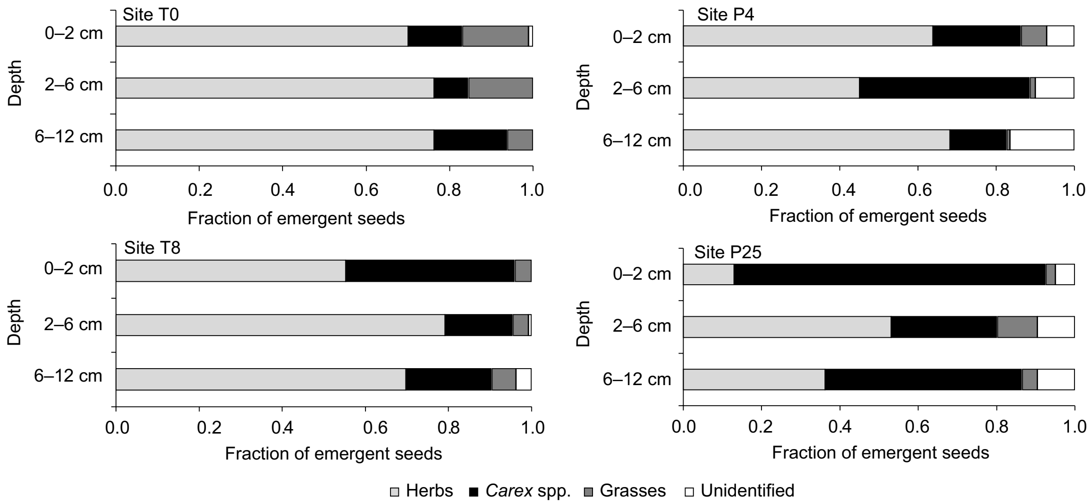

Fig. 2. Depth distribution of seeds in the soil profile. Species are grouped as follows: herbs, grasses, *Carex* spp. and unidentified seedlings. *Juncus* spp. and ruderal species were omitted (*see* text). The length of each bar section is proportional to the fraction of the total seeds present in that stratum which is represented by the respective group of species.

— found the highest densities of seeds on sites which were abandoned for five to six years.

High seed densities in soils of recently abandoned sites and a subsequent decrease in older fallows were also found on chalk grassland sites (Poschlod *et al.* 1991), and therefore the pattern might well be characteristic for abandoned grasslands in general.

One possible explanation for the phenomenon is that regular mowing limits growth and seed production of many grassland species (Maas & Schopp-Guth 1995, Falinska 1999).

In the abandoned wet meadows studied in this paper, as well as in those studied by Falinska (1999) and Jensen (1998), part of the temporary seed bank density increase after abandonment is due to a few species, above all *Juncus* spp. and *Carex* species.

When considering only grassland species, there are no significant differences in seed bank density between the sites. The apparent decrease in seed densities of grasses and grassland herbs with time since abandonment is compensated by an apparent increase in *Carex* species seed density. This is consistent with the known tendency within the latter group to accumulate a long-term persistent seed bank (Schütz 2000), although the persistence of some *Carex* species in the vegetation into later successional stages might also play a role.

There are only a few ruderal species present in small numbers in the seed banks of the sites T0 and T8. According to Rice (1989) who links the representation of seeds of fugitive species in the soil to grassland age this may indicate that these sites have been under grassland management for a long time without interruption. On the other hand, a number of ruderals had accumulated a persistent seed bank on the sites

Table 3. Similarity between the seed bank and the overlying plant community at a given site. Reverse phi-square similarity coefficients were calculated based on proportional frequency data (vegetation: number of quadrats in which a particular species is present divided by n = 25; seed bank: number of soil samples containing seeds of a particular species divided by n = 10 or, in case of site T8, n = 5).

Depth	T0	P4	T8	P25
0–2 cm	0.370	0.256	0.183	0.112
2–6 cm	0.350	0.207	0.222	0.072
6–12 cm	0.298	0.111	0.171	0.048
0–12 cm	0.343	0.225	0.239	0.098

P4 and P25. These include *Juncus bufonius*, *Plantago intermedia*, *Gnaphalium uliginosum*, *Sagina nodosa*, *Rorippa islandica*, *Polygonum arenastrum* and *Potentilla anserina*, all of which are typical weeds of wet arable land, and some also of goose pastures (Ellenberg 1996). How far this reflects previous land-use, as suggested by Thompson (1992), is not clear.

Alternatively, hydrochory might provide an explanation for the presence of seeds of these species. In a current study of meadows in Soomaa National Park, *Rorippa islandica*, *Potentilla anserina* and *Gnaphalium uliginosum* were among those species frequently found in strand line material deposited by the receding spring flood (A. Wanner pers. comm.).

It is worth mentioning that the emergence method rarely ever provides complete lists of species present in the seed bank (e.g. Falinska 1999). Some species present in the vegetation of the investigated sites might not have been detected in the soil samples simply because they maintain only a transient seed bank and therefore were absent from the seed bank at the time of sampling. On the other hand, it cannot be excluded that other species were not detected due to a lack of appropriate conditions for germination.

Vertical profile

Thompson's (1993) key was applied to the data to determine seed bank persistence types. As none of the sites had undergone any major disturbance (e.g. ice scouring) that could have disrupted the soil profile, the vertical distribution of seeds was a secure indicator of seed bank persistence. In the present study, this criterion was preferred over the criterion of a species "being present in the seed bank but absent from the established vegetation" (Thompson 1993), since the latter could have been caused by species' seeds being imported to a site by flooding. As species with only three or four seeds found in the samples of a single site could have a significantly heterogeneous depth distribution (e.g. *Leontodon autumnalis* or *Veronica longifolia* at the managed site T0), this number was considered to be sufficient for a provisional classification. This threshold is similar to that of Thompson *et al*. (1997).

Only a few characteristic wet grassland and fen species (*sensu* Ellenberg 1992) were classified as having a long-term persistent seed bank in this study, for example *Stachys palustris* and *Veronica scutellata*, which are poorly represented in the database of Thompson *et al*. (1997). Only one grass species, *Agrostis gigantea*, was classified as long-term persistent. The remaining grasses were either found to be short-term persistent or transient (*see* Appendix 1). These results are very similar to results of other studies summarised by Rice (1989) and Thompson (1992). A whole range of grassland herbs could be classified as short-term persistent in this study, among them *Viola epipsila*, which is absent from Thompson *et al*.'s (1997) seed bank database. Another species missing from the database, *Veronica longifolia*, was classified as transient. Seeds of the perennial *Filipendula ulmaria*, dominant in early successional vegetation, were only found in the seed bank of one site in very small numbers. This result is not surprising, as the vast majority of this species' records are classified as transient in Thompson *et al*.'s (1997) database.

The statistical analyses of the vertical distribution of individual species' seeds in the soil suggests that the depletion of a species' seed bank first takes place in the upper soil layers, which might be due to several factors, as there are (a) greater losses near the soil surface due to a greater readiness to germinate and/or a greater risk of predation or pathogens, and (b) translocation of seeds into deeper soil layers.

Comparison between seed bank and vegetation

The similarity between seed bank and vegetation composition is highest at the managed site, intermediate on the mid-term fallows and lowest at the longest abandoned site. Several factors contribute to this apparent decrease in similarity with time since abandonment. On the one hand, there are a number of grassland species lost from the vegetation but still present in the seed bank of the fallows. On the other hand, colonizing species such as *Salix* spp. remain absent from the seed bank. The presence of seeds of a number of ruderal species in the seed bank of two of the fallow sites, which do not occur in the overlying vegetation, also plays a role.

A decrease in similarity between vegetation and seed bank with time since abandonment is also reported from other studies on semi-natural grasslands (e.g. Jensen 1998, Kalamees & Zobel 1998). Thompson (2000) gives examples from other habitats, including successional old-fields.

The decrease in similarity between vegetation and seed bank with increasing soil depth found in this study is probably a common phenomenon and is known from other studies on semi-natural grasslands and their fallow stages (e.g. Milberg 1995) and other habitats (e.g. Grandin & Rydin 1998). At least two factors contribute to this pattern. One is the potentially greater rate of seed bank depletion in the upper soil layer, once a species has disappeared from the vegetation. The other is the fact that it takes some time for the seeds produced by recent colonizers to penetrate to lower soil layers.

Consequences for restoration

Twenty-two grassland, reedbed and fen species (*sensu* Ellenberg 1992) were classified as being at least short-term persistent in this study. Only a few of these species could be detected in the seed bank when lost from the vegetation, in which case seed densities were generally low. Only seven out of these 22 species were found to have a long-term persistent seed bank. A number of species from the vegetation were not detected at all in the seed bank, and at least some of these have to be considered as being transient.

These results correspond with the findings of a major study on soil seed banks in European grasslands (Bekker *et al*. 1997), indicating that restoration of species-rich grasslands is most worthwhile on grassland sites with a short history of biodiversity degradation.

We know of only one study on the resumption of management measures at abandoned semi-natural wet grassland sites, which explicitly considers the role of seed bank persistence in the interpretation of the results. In their study, Hald and Vinther (2000) found that species reacting positively to grazing differed significantly from the others by having a more persistent seed bank. However, mowing without additional grazing did not promote these species. Circumstantial evidence on the potential role of soil seed banks in the process of grassland restoration might also be derived from an experiment on the restoration of overgrown wet semi-natural grassland in Sweden. In that study (Milberg 1994), several of the species classified by us as long-term persistent or short-term persistent increased their cover after the application of rotavation (e.g. *Potentilla anserina*, *Myosotis scorpioides*, *Mentha arvensis*, *Galium uliginosum et palustre* agg.), and others recolonized the treatment plots (e.g. the ruderals *Rorippa palustris*, *Polygonum aviculare* and *Juncus bufonius*).

The above studies emphasize the role of disturbance in the activation of the soil seed bank. Dominant tall herbs of overgrown stages, such as *Filipendula ulmaria*, tend to form dense litter layers (Ellenberg 1996). In the presence of such litter layers, restoration of a species-rich grassland from the seed bank requires the breaking-up of the litter to avoid substantial delays caused by the slow rate of natural decomposition (Balsberg 1982). A customary practice is litter-stripping. This practice has proved to effectively release the dormant seed bank in the top few cm of soil in wet meadows (Špačková *et al*. 1998), and Mitchell *et al*. (1998) also recommend it for heathland restoration. Additionally, it also reduces the effect of nutrient accumulation (Mitchell *et al*. 1998), which usually occurs after abandonment of wet grasslands (Müller *et al*. 1992).

Given the transient nature of the seed bank of many species, it is obvious that the seed bank can only provide propagules of a limited number of species for the restoration of meadow communities. Other species, if not reintroduced, depend on the slower processes of recolonization.

In some cases, e.g. in the studied area, seed dispersal by the natural flooding regime (regular spring flooding, plus occasional summer or autumn flooding) might assist this immigration process. If possible, the (re)introduction of light aftermath grazing might also enhance species diversity. Apart from creating disturbance and thus facilitating seedling recruitment, cattle grazing promotes seed dispersal of many grassland species (Stender *et al*. 1997). An appropriate mowing regime can have similar effects, since a number of species are dispersed by mowing machinery (Bakker *et al*. 1995, Strykstra *et al*. 1997). Any of these measures however depend on the presence of extant species-rich meadows which act as propagule donors. Therefore, absolute priority should be given to the maintenance of remaining species-rich meadows.

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Appendix 1. Composition of the seed bank of the investigated sites. Persistence types after Thompson *et al.* (1997): T = transient, SP = short-term persistent, LP = long-term persistent, nc = not classified. Also shown are the classification criteria, i.e. presence/absence in the vegetation (indicated by +/–) and number of emerged seedlings calculated as seedlings/m^2 including depth distribution (– = seedlings absent). Presence of a species in the seed bank whilst being absent in the vegetation of a site is indicated by bold seedling numbers. The vegetation type in which a species mainly occurs (from Ellenberg 1992) is also indicated: D = disturbed habitats, G = grassland, R = reedbeds & fens, W = woodland & scrub, u = unclassified. Note that seedling numbers from site T8 are calculated from 5 pooled soil samples only (instead of 10).

Taxa	Primary community	Persistence type	Present in vegetation				Seedling density/m^2 over the sampled profile (in 0–2 cm, 2–6 cm, 6–12 cm depths)			
			T0	P4	T8	P25	T0	P4	T8	P25
Agrostis gigantea	G	LP	+	+	–	–	80 (8, 40, 32)	64 (48, 8, 8)	**159 (48, 64, 48)**	**95 (0, 88, 8)**
Gnaphalium uliginosum	D	LP	–	–	–	–	–	**517 (24, 127, 366)**	–	–
Juncus articulatus	R	LP	–	–	–	–	–	**859 (32, 310, 517)**	**1130 (143, 573, 414)**	**16 (0, 16, 0)**
Juncus bufonius	D	LP	–	–	–	–	–	**2570 (398, 1416, 756)**	–	**1464 (183, 406, 875)**
Leucanthemum vulgare	G	LP	–	+	–	–	–	127 (0, 40, 88)	–	–
Luzula campestris	G	LP	+	+	–	–	517 (72, 167, 279)	286 (119, 159, 8)	**48 (16, 0, 32)**	**8 (0, 0, 8)**
Plantago intermedia	D	LP	–	–	–	–	–	**1186 (80, 446, 660)**	–	–
Polygonum arenastrum	D	LP	–	–	–	–	–	**32 (0, 0, 32)**	–	–
Potentilla anserina	D	LP	–	+	+	–	–	24 (8, 16, 0)	–	**183 (8, 151, 24)**
Rorippa islandica	D	LP	–	–	–	–	–	**255 (0, 24, 231)**	–	**541 (48, 470, 24)**
Sagina nodosa	D	LP	–	–	–	–	–	**390 (40, 215, 135)**	–	**16 (0, 16, 0)**
Stachys palustris	G	LP	+	–	+	+	127 (0, 8, 119)	–	–	8 (0, 8, 0)
Trifolium repens	G	LP	–	+	–	–	–	103 (8, 48, 48)	**32 (0, 0, 32)**	**8 (0, 0, 8)**
Veronica scutellata	R	LP	+	–	–	–	103 (0, 72, 32)	–	**350 (0, 255, 95)**	**565 (8, 454, 103)**
Campanula patula	G	SP	–	+	–	–	–	565 (127, 255, 183)	–	–
Cardamine pratensis	G	SP	+	+	+	+	–	–	–	32 (0, 16, 16)
Carex pallescens	G	SP	+	+	–	–	135 (16, 48, 72)	167 (16, 151, 0)	–	–
Carex panicea	R	SP	+	+	+	–	175 (40, 40, 95)	931 (231, 613, 88)	255 (95, 111, 48)	–
Cerastium fontanum	G	SP	+	+	–	–	16 (16, 0, 0)	88 (40, 40, 8)	–	–
Deschampsia cespitosa	u	SP	+	+	+	–	350 (183, 143, 24)	40 (32, 8, 0)	32 (16, 16, 0)	**80 (16, 56, 8)**
Festuca rubra	G	SP	+	+	–	–	48 (0, 32, 16)	–	–	–
Galium palustre	R	SP	+	–	+	+	8 (8, 0, 0)	–	–	127 (32, 88, 8)
Galium uliginosum	G	SP	+	+	+	–	151 (72, 56, 24)	103 (8, 72, 24)	318 (64, 191, 64)	**16 (0, 8, 8)**
Juncus filiformis	G	SP	–	–	+	–	–	–	28266 (7066, 13274, 7926)	–
Lychnis flos-cuculi	G	SP	+	+	–	–	247 (80, 103, 64)	127 (16, 64, 48)	32 (0, 16, 16)	–
Lythrum salicaria	G	SP	–	–	+	+	–	–	32 (0, 16, 16)	111 (64, 32, 16)
Mentha arvensis	u	SP	+	+	–	+	–	183 (32, 64, 88)	–	48 (0, 40, 8)
Myosotis scorpioides	G	SP	+	–	–	–	8 (0, 8, 0)	–	**95 (32, 48, 16)**	–
Potentilla erecta	G	SP	+	+	+	–	223 (32, 127, 64)	–	16 (0, 16, 0)	–
Ranunculus auricomus	W	SP	+	+	+	–	119 (16, 88, 16)	111 (0, 111, 0)	780 (223, 430, 127)	–
Viola canina	G	SP	+	+	–	–	724 (64, 366, 294)	175 (143, 32, 0)	**16 (8, 8, 0)**	**72 (0, 64, 8)**
Viola epipsila	R	SP	–	–	+	–	–	–	127 (16, 80, 32)	–

Achillea ptarmica	G	T	+	+	+	–	24 (16, 8, 0)	–	–	–
Anthoxanthum odoratum	u	T	+	+	+	–	16 (16, 0, 0)	16 (16, 0, 0)	–	–
Centaurea jacea	G	T	+	+	–	–	16 (16, 0, 0)	8 (0, 8, 0)	–	–
Filipendula ulmaria	G	T	+	+	+	+	–	–	48 (0, 32, 16)	–
Geum rivale	G	T	+	+	+	–	–	16 (8, 8, 0)	16 (0, 0, 16)	–
Leontodon autumnalis	G	T	+	–	–	–	24 (24, 0, 0)	–	–	–
Poa pratensis	G	T	+	+	–	–	64 (16, 48, 0)	–	–	–
Veronica longifolia	G	T	+	–	–	–	32 (32, 0, 0)	–	–	–
Artemisia vulgaris	D	nc	–	–	–	–	–	–	**32 (0, 0, 32)**	–
Cirsium arvense	D	nc	–	–	–	–	**8 (0, 8, 0)**	–	**32 (32, 0, 0)**	–
Cirsium palustre	G	nc	–	–	–	–	–	–	**16 (16, 0, 0)**	–
Lycopus europaeus	R	nc	–	–	–	+	–	–	–	24 (8, 16, 0)
Lysimachia vulgaris	u	nc	+	–	+	+	8 (0, 8, 0)	–	–	–
Phleum pratense	G	nc	+	+	–	–	–	–	–	8 (0, 0, 8)
Polemonium caeruleum	G	nc	–	+	–	–	–	16 (16, 0, 0)	–	–
Scutellaria galericulata	R	nc	–	–	+	–	–	–	–	8 (8, 0, 0)
Scutellaria hastifolia	G	nc	–	–	–	–	–	–	**16 (0, 16, 0)**	–
Selinum carvifolia	G	nc	+	–	–	–	8 (0, 8, 0)	–	–	–
Other *Carex* species agg.		(SP)					294 (143, 88, 64)	477 (111, 318, 48)	828 (462, 239, 127)	2037 (1027, 589, 422)
Carex acuta	R		–	–	–	+				
Carex acutiformis	u		+	–	–	+				
Carex cespitosa	R		–	–	+	+				
Carex disticha	R		+	–	+	+				
Carex flava	R		–	+	–	–				
Carex hartmannii	G		–	+	–	–				
Carex nigra	R		+	+	–	–				
Carex riparia	R		–	–	–	+				
Carex vesicaria	R		–	–	–	+				
Carex vulpina	R		–	–	–	+				
R. acris et repens		(SP)					1249 (589, 557, 103)	844 (493, 215, 135)	1146 (477, 573, 95)	263 (16, 231, 16)
Ranunculus acris	G		+	+	+	–				
Ranunculus repens	u		+	+	+	+				
S. graminea et palustris		(SP)					32 (24, 8, 0)	–	64 (32, 0, 32)	334 (32, 199, 103)
Stellaria graminea	u		+	+	–	–				
Stellaria palustris	R		+	–	+	+				
Other Poaceae agg.							80 (16, 56, 8)	24 (8, 16, 0)	–	103 (16, 80, 8)
Other monocots spp. agg.							–	88 (16, 40, 32)	–	64 (8, 48, 8)
Dicots spp. agg.							16 (16, 0, 0)	422 (95, 207, 119)	48 (0, 16, 32)	286 (56, 159, 72)
Total							**4902 (1512, 2085, 1305)**	**10815 (2165, 5029, 3621)**	**33 948 (8754, 15 979, 9215)**	**6517 (1528, 3231, 1759)**

Appendix 2. List of species present in vegetation which were not found in the seed bank of any site. Species are listed in alphabetical order. Additional information regarding the occurrence at single sites is given in brackets.

Achillea millefolium (T0, P4), *Alchemilla vulgaris* agg. (T0,P4), *Alopecurus pratensis* (T0, T8), *Angelica sylvestris* (all sites), *Avenula pubescens* (P4), *Briza media* (P4), *Calamagrostis canescens* (T0, P25), *Calamagrostis stricta* (P4, P25), *Caltha palustris* (T0, T8, P25), *Carum carvi* (P4), *Cirsium helenioides* (T0, P4), *Cirsium oleraceum* (P4), *Dactylis glomerata* (P4), *Epilobium palustre* (P25), *Festuca ovina* agg. (P4), *Festuca pratensis* (T0, P4), *Frangula alnus* (P4), *Galium boreale* (T0, P4, T8), *Galium mollugo* (T0, P4), *Geranium palustre* (T0), *Geranium pratense* (T0), *Glechoma hederacea* (T0), *Hieracium pilosella* aff. (P4), *Hieracium umbellatum* (P4), *Hypericum maculatum* (P4), *Iris pseudacorus* (T0, T8, P25), *Iris sibirica* (T0), *Lathyrus pratensis* (T0, P4, T8), *Parnassia palustris* (P4), *Peucedanum palustre* (T8), *Phalaris arundinacea* (P25), *Plantago lanceolata* (P4), *Potentilla palustris* (T8, P25), *Prunella vulgaris* (T0, P4), *Rumex acetosa* (T0, P4), *Salix cinerea* (all sites), *Salix pentandra* (P4, T8, P25), *Salix rosmarinifolia* (P4), *Salix triandra* (P4, T8), *Senecio paludosus* (T8, P25), *Sesleria caerulea* (T0, P4), *Sium latifolium* (P25), *Symphytum officinale* (T0), *Thalictrum flavum* (P25), *Trifolium pratense* (T0, P4), *Trollius europaeus* (T0, P4), *Valeriana officinalis* (T0, P4, T8), *Veronica chamaedrys* (P4), *Vicia cracca* (T0, P4, T8), *Vicia sepium* (T0, P4)