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Restoration of the *Cirsio dissecti-Molinietum* in The Netherlands: Can we rely on soil seed banks?

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Abstract. Vegetation and soil seed banks of a threatened Atlantic fen meadow community were studied using recent phytosociological records and seedling emergence from soil samples. Similarly managed but differently degraded stands that suffered different levels of species impoverishment were compared. The actual vegetation was related to a set of phytosociological references representing the subassociations of the community. DCA positions of reference relevés from the different subassociations were overlapping, suggesting that in all references many common species occur. Recent records were positioned in-between the seed bank samples and the references. The soil seed banks of all stands were dominated by ordinary species. Most character species had at most sparse seed banks and no seedlings of locally extinct character species, mentioned in historic floristic records, were detected. In contrast species of pioneer and small-sedge communities as well as those of heathlands were abundant in the seed banks. Based on the vertical distribution of seeds in the soil layers most fen meadow species were classified into transient or short-term persistent seed bank types. We concluded that complete restoration of the *Cirsio dissecti-Molinietum* without reintroduction is only likely in stands that were degraded only a few years ago. On the other hand, the presence of viable seeds of *Nanocyperion* and *Parvocaricetea* species is promising for the restoration of these communities even after decades. Recreation of pioneer habitats by sod cutting will preserve these species.

Keywords: Fen meadow; Fragmentation; Historic vegetation data; Junco-Molinion; Red List species; Seed longevity; Seedling emergence.

Nomenclature: van der Meijden (1996) for taxa; Schaminée et al. (1996) for syntaxa.

Abbreviations: DCA = Detrended Correspondence Analysis; EXV = Eexterveld; ULE = Ule Krite; WYL = Wyldlannen; WTS = Wijnjeterperschar.

Introduction

The *Cirsio dissecti-Molinietum* (Sissingh 1978) is a low-productive, species-rich fen meadow community that has its main distribution in the NW European lowlands and is restricted to an area with Atlantic climatic influences (Zijlstra 1981; Rodwell 1991; Schaminée et al. 1996; Blackstock et al. 1998). The typical semi-natural litter meadow develops on base-rich, nutrient-poor, wet soils supported either by discharge of ground water or by inundation of calcareous surface water (Spieksma et al. 1995). The management consists of late summer cutting or grazing (Blackstock et al. 1998; Hayati & Proctor 1990). A low nutrient availability is maintained by seasonally high water tables, which reduce mineralization rates and stimulate the formation of iron and calcium-phosphate complexes (Koerselman & Verhoeven 1995; Boeye et al. 1996; Boyer & Wheeler 1989; Jansen et al. 2000, 2001).

In The Netherlands the community once occupied several thousands of hectares . Nowadays, well-developed *Cirsio-Molinietum* stands have been reduced to ca. 30 ha in total due to large-scale land reclamations in the 1950s and 1960s which have changed both the hydrological and nutrient conditions (Westhoff 1979; Schaminée et al. 1996). Several small remnants are kept as nature reserves which occur scattered in an intensively managed agricultural landscape. Drainage of surrounding agricultural fields, groundwater abstraction as well as increased atmospheric N-deposition resulted in drier and more eutrophic conditions. This led to further degradation of mesotrophic fen meadow sites during the last few decades (Smeets et al. 1980; Grootjans et al. 1986; Buck-Sorlin 1993). All sites are threatened by increased acidification and species impoverishment (Jansen et al. 1996; Rossenaar & Streefkerk 1997).

Various measures have been carried out to restore degraded fen meadows. Common measures are rewetting and sod cutting (Koerselman 1989; Jansen et al. 1996; Jansen & Roelofs 1996). Rewetting is done by increasing

water levels in the surroundings of the reserve, while sod cutting is carried out to remove the degraded topsoil. Although some successes have been reported in restoring abiotic conditions in degraded fen meadows (Jansen et al. 2000, 2001), e.g. by formation of buffer zones around the reserves or restoring the hydrological system on a larger scale, failures have also been presented (Jansen et al. 1996; van Duren et al. 1998). In such cases only species-poor communities re-established and the pioneer phase was not followed by a complete regeneration of the fen meadow community (Jansen & Roelofs 1996). No complete regeneration of *Cirsio dissecti-Molinietum* has been realized until now (Jansen et al. 1996).

Lack of viable seeds of characteristic species in the soil seed bank was hypothesized to be partly responsible for these unsatisfactory results (Jansen et al. 2000). However, we have little information on seed bank characteristics of mesotrophic fen meadow communities (Thompson et al. 1997; Bekker et al. 1998; Prins et al. 1998). Seed bank analyses of *Cirsio dissecti-Molinietum* stands are only available for England (Tallowin & Smith 1996) and The Netherlands (van Duren et al. 1998; Matus et al. 2001). Our aim was to investigate the seed bank formation in fen meadows situated in the centre of its geographical region, where restoration is most needed. For this reason we compared the seed bank composition of various degraded sites with their present vegetation and also with reference descriptions of undisturbed fen meadows of the past. The research aims to assess the seed longevity of the characteristic species of the community to provide a better understanding of the successes and failures achieved in restoration projects.

Methods

Study area

Seed banks and vegetation composition were studied in four fen meadow reserves in the northern part of The Netherlands (Table 1). These sites harboured well-developed *Cirsio-Molinietum* in the past and nowadays they are still managed traditionally. Some of these reserves have been negatively affected by deep drainage in surrounding agricultural areas and acidification and have floristically impoverished during the last decades.

Table 1. Code, position, extension and basic soil characteristics of the recently sampled stands.

Code	Site	Geo-coordinates	Area (ha)	Soil type
WTS	Wijnjeterperschar	53°02' N, 6°10' E	1.25	Peat
ULE	Ule Krite	53°07' N, 5°55' E	0.40	Peat on sand
WYL	Wyldlannen	53°07' N, 5°55' E	0.25	Peat on clay
EXV	Eexterveld	53°01' N, 6°41' E	0.05	Peat on sand

Seed bank sampling

Soil seed banks were sampled in April, after winter stratification but before spring germination. The samples were taken from Ule Krite (ULE) and Wyldlannen (WYL) in 1994 and from Wijnjeterperschar (WTS) and Eexterveld (EXV) in 1999.

At WTS and EXV ten $2 m \times 5 m$ plots were sampled. The small size of the EXV stand required sampling of contiguous plots. Two groups of contiguous plots were applied at the WTS in order to limit soil disturbance to a small part of the stand by shortening sampling routes. At the other two stands, where no such constraints prevailed, randomly selected non-contiguous plots were studied. Ten $10 m \times 10 m$ plots were chosen in the WYL whereas nine $8 m \times 8 m$ sized plots were sampled in ULE. At all stands ten soil cores of 4 cm diameter were drilled in each plot resulting in 90 cores in ULE and 100 cores in the other three sites.

Samples at WTS and EXV were 10 cm deep and were subdivided into 0 - 5 cm and 5 - 10 cm layers. In the other two stands 20 cm deep cores were drilled which were divided into 0 - 10 cm and 10 - 20 cm layers. In order to obtain comparable data sets, only the results from the 0 - 10 cm layers are discussed – i.e. the total volume of samples amounted to 11309 cm^3 at ULE and 12566 cm^3 at the other sites. However, data on the vertical distribution of seeds published in van Duren et al. (1998) and Matus et al. (2001) were used to determine the seed bank types according to Thompson et al. (1997).

The ten cores taken from the same layer of a plot were pooled on the spot and treated together. Samples were concentrated with a bulk reduction procedure, which also promotes germination (by freeing seeds from soil particles, by slight scarification of seed coats and by washing out inhibitors; ter Heerdt et al. 1996). Coarse material was removed by washing the samples over a sieve of 4.0 mm mesh width, while clayey and silty components were removed by washing the samples over a fine sieve (mesh width 0.212 mm). Except for orchid seeds, practically all seeds could be captured using this methodology.

Concentrated samples were spread on $30 cm \times 30 cm$ trays that were previously filled with 4 cm of normal and 4 cm of steam-sterilized potting soil and then covered by a thin layer of sterilized sand. ULE and WYL samples were placed into a temperature-controlled greenhouse where temperature varied between 25/15 °C (day/night). Extra light was supplied in periods when the amount of natural light was insufficient. Samples from EXV and WTS were placed in a climate chamber and illuminated for 12 hours a day. Temperature fluctuation was set to 23/16°C (day/night).

Germination lasted for 14 weeks. Watering of ULE and WYL samples was stopped after seven weeks when only a small number of new seedlings emerged. The 3-4 mm thick sample layers were crumbled after a week's drying and turned in order to facilitate the germination of deep lying seeds. Their germination was followed for another seven weeks. In the case of the WTS and EXV samples, spread in 1-2 mm thin layers, light penetration was considered to be sufficient. Here sample layers were kept intact during 14 weeks. No new species emerged after 10 weeks and germination rate dropped as low as 1-2 seedlings/week after 12 weeks therefore germination was thought to reach a sufficiently representative level.

Seedlings were usually grown in the trays until they could be identified (Csapody 1968; Muller 1978). They were then counted and removed with minimal disturbance to the germination medium. Seedlings of unidentified taxa were transplanted into pots with normal soil and placed in the greenhouse. Non-flowering transplants of problematic taxa were transferred to the experimental garden onto open-air tables and were identified later. Seedlings of *Juncus effusus*/*J. conglomeratus* and *Cirsium palustre*/*C. × forsteri* were not fully distinguishable, and therefore lumped. Specific dominance in *Agrostis* and *Carex* species was calculated after a representative portion of their seedlings was transplanted and determined. Control trays, without adding samples, were used to detect accidental seed rain. Species found in these trays (mostly seedlings of the greenhouse weed, *Spergularia rubra*), occurred sporadically also in sample trays and were excluded from analyses.

Actual and historic vegetation

The vegetation was recorded in the summer of the same year in which the seed bank was sampled. Species cover (%) was estimated in five 2 m × 2 m plots, overlapping with the seed bank plots and scattered in the stands. Species in the direct vicinity of the plots were also noted and indicated with (e), meaning extra. In order to assess the period of extinction of certain characteristic species, historic floristic records have been collected for all sites for the exact locality of sampling and the close (< 250 m) vicinity. The various sources of mostly unpublished data are all available upon request at the second author.

As a phytosociological reference we used historic relevés from the Dutch National Vegetation Database (Schaminée et al. 1996). Relevés representative of those three subassociations of the community still present in the northern region of The Netherlands where our study sites are located (i.e. *nardetosum*,

typicum, *peucedanetosum*; Zuidhoff et al. 1996), were selected from this database. The selection was based on the following criteria:

1. The variation of the subassociation within the phytogeographic region of the study site should be represented. In order to avoid emphasizing local features only one relevé per site for each subassociation was selected.
2. Similar plot sizes were chosen to minimize the effect of area-species number relationships. Size of all relevés was < 10 m^2.
3. Minimal personal effect; relevés made by different surveyors were preferred.
4. Similarly aged, relatively new references were chosen so as to compare recent state of *Cirsio-Molinietum* subassociations to our surveys. The average date of the relevés for a subassociation was between 1982 and 1990 and only relevés taken after 1965 were used.

Data processing

Detrended correspondence analyses (DCA) were performed using the software package CANOCO (ter Braak 1995). Prior to analysis traditionally scaled cover estimates were transformed to the percentage scale by the software package Turboveg for Windows (Hennekens 1999). Partly identified taxa were pooled with their fully determined pairs (e.g. *Betula* spec. with *B. pubescens*). No subspecies or varieties were distinguished. Species detected only at a single site with low frequencies either in the vegetation (one plot; < 1% cover) or in the seed bank (< 3 seedlings) were not involved in the multivariate analyses. Pteridophytes and orchids could not be determined in the seed bank and were also excluded from the DCA. Means of number of species and that of seedlings were compared between sites with *t*-tests or Welch-tests after testing the equality of variance with *F*-tests (Zar 1999). The normality of distribution prior to the analyses was determined with the Kolmogorov-Smirnov test.

Results

Seed banks

The seed bank composition differed largely between the four sites. Out of a total number of 83 species, only eight occurred in all sites, and only nine were found in three out of four localities. The highest number of taxa was found in the two Pleistocene sites (WTS and EXV) where also the number of characteristic fen meadow species (*Junco-Molinion*) was highest. The average number of taxa per plot was highest in the EXV site and lowest in the Holocene WYL site. The number of germinated seeds varied significantly between and also within sites (Table 2a). Rough estimates of seed densities (i.e. calculated without taking spatial pattern into account) ranged from 25000.m^{-2} (WYL) to 140000.m^{-2} (ULE).

A limited number of species built up the vast majority of the local seed bank. Due to the strong dominance of *Juncus conglomeratus/effusus* in three of the sites, most samples were closely positioned in the DCA-plot (Fig. 1). The *Agrostis canina* dominated WYL samples were plotted further from the core. The most abundant species contributed 47 - 91% of the local seed bank while the summed dominance of the five most common taxa varied between 88% and 97%. Four common taxa, *Juncus conglomeratus/effusus*, *J. bulbosus*, *J. articulatus*

and *Agrostis canina*, were dominating in every site though with large variation (Table 3, below). Some species were only locally frequent.

Most species were present in the vegetation as well as in the seed bank. Only a few species that were present in the vegetation were apparently lacking from the seed bank, e.g. *Salix* spp., *Peucedanum palustre*, *Succisa pratensis*. Some species that were dominant in the vegetation tended to form sparse seed banks: *Molinia caerulea* and *Cirsium dissectum*. In contrast, some taxa that were rare in the vegetation sometimes had large seed banks: *Juncus conglomeratus/effusus* and *Ranunculus repens*. *Juncus articulatus*, *J. bufonius*, *J. bulbosus* and *Myosotis laxa* were missing in the vegetation but were present in the seed bank in large quantities (Table 3, below).

Viable seeds of characteristic fen meadow (*Cirsio dissecti-Molinietum*) species were rare in all seed banks. In general the species of the moist grassland communities (*Molinio-Arrhenatheretea*) contributed little to the seed banks, although many of these contributed significantly to the vegetation. In contrast, species of small sedge communities (*Carex curta*, *Veronica scutellata*), pioneer communities (*Isolepis [Scirpus] setaceus*, *Chenopodium album*, *Conyza [Erigeron] canadensis*) and heathlands (*Calluna vulgaris*, *Carex pilulifera*, *Juncus squarrosus*) were only detected in the seed bank but not in the actual vegetation. In general, species of small

Table 2. Number of taxa characteristic of selected phytosociological groups (Zuidhoff 1996), total number of taxa and mean number of taxa/plot: (**a**) in soil seed bank (mean number of seedlings/plot); (**b**) in vegetation. Total species number in vegetation and seed bank as well as number of species common to vegetation and seed bank, respectively, is also shown. Letters refer to significant ($p < 0.05$) differences based on the *t*-test or Welch-test.

a. Seed bank	WTS	EXV	ULE	WYL
Junco-Molinion	2	3	2	1
Molinio-Arrhenatheretea	11	9	5	2
Parvocaricetea	8	3	10	8
Isoeto-Nanojuncetea	2	1	1	1
Total in seed bank	42	41	36	23
Mean species no./plot ($n = 10$)	21.3[b]	25.0[a]	19.0[b]	11.3[c]
Mean seedling no./plot ($n = 10$)	895.3[b]	820.4[b]	1752.0[a]	321.2[c]
b. Vegetation	WTS	EXV	ULE	WYL
Junco-Molinion	5	5	3	1
Molinio-Arrhenatheretea	15	11	3	5
Parvocaricetea	9	4	9	5
Isoeto-Nanojuncetea	1	0	0	1
Species number in plots	35	28	28	25
Extra-plot species	10	8	1	1
Total in vegetation	45	36	29	26
Mean species number/plot ($n = 5$)	21.0[a]	17.0[a]	20.0[a]	11.0[b]
Total in vegetation and seed bank	52	53	48	34
Common to vegetation and seed bank	35	26	18	16
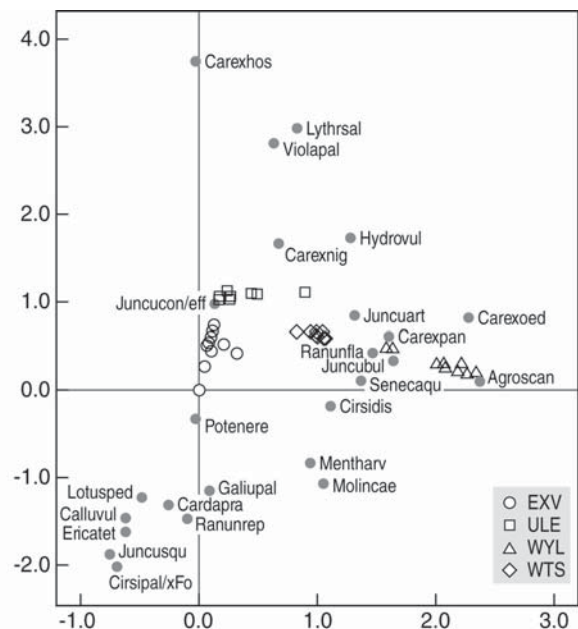
Fig. 1. Results of Detrended Correspondence Analysis; ordination of dominance data of seed bank records. Frequent (> 0.5 %) and character species present at more than one site are shown. (See Table 1 for codes of site names.)

sedge communities (*Parvocaricetea*) such as *Carex nigra*, *C. echinata*, *C. oederi*, *Hydrocotyle vulgaris*, *Juncus articulatus*, *Ranunculus flammula*) contributed significantly to the seed banks, although they were subordinates in the vegetation (Table 4).

Actual vegetation

Out of the totally recorded 74 vascular taxa 11 were found at three sites and only seven species occurred at all sites. The number of species in sample plots as well as the total number in the vegetation (i.e. including species in extra plots) was highest at WTS and lowest at WYL (Table 2b). The number of *Junco-Molinion* species was apparently higher at WTS and EXV than at other stands. The average number of taxa per plot was significantly ($p < 0.05$) lower at WYL than elsewhere (Table 2b). Most of the species had a low percentage cover. Only three species (*Agrostis canina*, *Carex panicea*, *Molinia caerulea*) had > 10% cover at more than one site and further 13 taxa had > 5% cover at least at one site. (Table 3).

Floristic change

Local species pools at WTS, ULE and EXV were impoverished in different degrees as shown by the loss of character species in the plots and in their close vicinity. In WTS the process had started in the 1960-1970s while the degradation of the other two stands had commenced already 50 - 60 yr ago. Loss of some non fen meadow species, indicators of hygrophilous conditions, also suggests desiccation of the latter two sites. Although the number of documented species extinctions was low, the earliest and most severe diversity loss happened at the Holocene site WYL, where most character species had already disappeared more than 60 yr ago (Table 5).

Comparison with reference relevés

In the DCA-plot the reference relevés were not grouped according to the subassociations but had largely overlapping positions (Fig. 2, below), indicating that despite their differences, they shared many species. Vegetation of the sites was more related to the references than to the seed banks. Recent relevés from all sites formed compact, distinct patches and were plotted between their seed bank samples and the references. ULE and WYL were the most similar sites, both regarding their actual vegetation composition and their seed bank.

Table 4. Dominance (%) of selected phytosociological groups (Zuidhoff 1996) in seed bank and vegetation samples. Calculations are based on seedling counts and estimates of specific cover in vegetation, respectively. (See Table 1 for codes of site names.)

	WTS	EXV	ULE	WYL
Seed bank				
*Molinio-Arrhenatheretea**	1.7	2.1	0.1	1.3
*Junco-Molinion**	0.4	0.1	<0.1	1.0
Juncus conglomeratus/effusus	46.8	79.0	91.2	0.6
Parvocaricetea	30.7	3.0	6.0	69.2
Agrostis canina	19.1	2.7	2.9	65.1
Isoeto-Nanojuncetea	18.4	0.6	0.8	19.0
Vegetation				
*Molinio-Arrhenatheretea**	42.2	21.3	35.5	3.2
*Junco-Molinion**	35.7	14.6	35.5	0.9
Juncus conglomeratus	8.1	2.7	2.0	0.3
Juncus effusus	0.0	5.0	1.3	0.3
Parvocaricetea	24.3	5.0	21.4	43.2
Agrostis canina	13.0	2.6	2.3	40.4
Isoeto-Nanojuncetea	0.0	0.0	0.0	0.3

* exclusive *Juncus conglomeratus*.

Table 5. Historic records of selected taxa, last published date (yr) of presence. Codes: x = recently confirmed, (x) = almost extinct, * = within 250 m distance to the site, - = not recorded. CM = *Cirsio-Molinietum* (*Junco-Molinion*), CA = *Calthion*, MA = *Molinio-Arrhenatheretea*, PC = *Parvocaricetea*, IN = *Isoeto-Nanojuncetea*, OS = *Oxycocco-Sphagnetea*, SC = *Scheuchzerietea*. (See Table 1 for codes of site names.)

species	coenology	WTS	EXV	ULE	WYL
Carex buxbaumii	CM	1986	-	-	-
Carex dioica	PC	1957	-	-	-
Carex echinata	PC	1957	-	x	x
Carex hostiana	CM	x	(x)	x	(x)
Carex pulicaris	CM	x	x	-	-
Cirsium dissectum	CM	x	x	x	*
Cirsium palustre	MA	x	x	1948	-
Gentiana pneumonanthe	OS	x	x	x	-
Hydrocotyle vulgaris	PC	x	x	x	x
Menyantes trifoliata	SC	-	-	1948	-
Parnassia palustris	PC	-	*	-	-
Pedicularis sylvatica	OS	-	*	-	-
Polygala serpyllifolia	OS	-	*	-	-
Potentilla palustris	PC	x	*	-	-
Senecio aquaticus	CA	x	-	1948	-
Succisa pratensis	CM	x	x	1948	-
Trichophorum cespitosum	OS	-	*	-	-
Viola persicifolia	CM	-	-	-	x

Table 3. Detailed vegetation and seed bank data. Species were first grouped according to their presence in vegetation/seed bank (0 - 10 cm) samples then ranked following a decreasing dominance in seed bank. Vegetation: mean cover (VMC; %); frequency (Vfr: I - V = 1-5 plots), e = 'extra-plot species' near the plots; p = species present further from plots. Seed bank: number of seedlings (No. sl.); frequency (Sfr; I = 1 - 2, ..., V = 9 - 10 plots). Phytosociological code (Code): CM = *Cirsio-Molinietum (Junco-Molinion),* CA = *Calthion*; MO = *Molinietalia*; MA = *Molinio-Arrhenatheretea*; PC = *Parvocaricetea*; IN = *Isoeto-Nanojuncetea*.

Code	Species	Wijnjeterperschar				Eexterveld				Ule Krite				Wyldlannen			
		VMC	Vfr	No.sl.	Sfr	VMC	Vfr	No.sl.	Sfr	VMC	Vfr	No.sl.	Sfr	VMC	Vfr	No.sl.	Sfr
	Mostly in vegetation																
	Salix repens	11,0	V	1	I												
	Festuca ovina	1,0	III	1	I												
CM	*Succisa pratensis*	0,6	III			0,4	II	1	I								
CM	*Carex hostiana*	2,4	III				e			1,0	IV						
	Eriophorum angustifolium	0,4	II							5,4	V			0,8	IV		
	Salix cinerea	0,2	I			38,0	V			0,8	III						
	Peucedanum palustre					0,4	II			0,2	I			0,2	I		
	Carex lasiocarpa									4,6	V						
	Iris pseudacorus									0,8	IV						
	Filipendula ulmaria									0,6	III						
PC	*Pedicularis palustris*									0,4	II						
	Phragmites australis									1,2	V			1,4	V		
CA	*Rhinanthus angustifolius*													0,4	II		
	Chamaenerion angustifolium													0,2	I		
	In vegetation and seed bank																
	Leontodon autumnalis	0,4	II	31	III												
MA	*Centaurea jacea* s.l.	1,0	II	27	IV												
MO	*Valeriana dioica*	4,4	III	16	II												
MO	*Galium uliginosum*	0,4	II	2	I												
MA	*Prunella vulgaris*	0,2	I	1	I												
MO	*Luzula multiflora*		e	3	I	0,4	II										
	Ranunculus repens	2,0	IV	42	V	0,2	I	216	V								
	Mentha arvensis agg.	3,0	IV	31	IV	0,2	I	19	II								
CA	*Lotus pedunculatus*	0,8	IV	3	II	2,2	V	45	V								
	Betula pubescens			1	I	0,4	II	33	IV								
	Agrostis tenuis					0,2	I	3	II								
MO	*Achillea ptarmica*					0,2	I	2	I								
MA	*Cerastium fontanum* ssp. *vulgare*							3	I						e		
MO	*Cirsium palustre*					4,8	V	31	V					0,8	II		
CM	*Cirsium* × *forsteri*					0,2	I										
	Lycopus europaeus		e	3	II	1,4	V	88	V		e						
MA	*Holcus lanatus*	0,2	I	23	III	0,4	II	35	V			2	I				
CM	*Cirsium dissectum*	6,4	V	6	III	10,0	V	1	I	2,8	V	1	I				
	Anthoxanthum odoratum	0,6	III	13	III	0,2	I	57	V			2	I				
MA	*Cardamine pratensis*	0,2	I	5	II	0,4	II	47	V			1	I	0,4	II		
	Potentilla erecta	0,2	I	1	I	1,6	IV	16	IV	0,6	III	28	V				
MO	*Juncus conglomeratus*	9,0	V	4188	V	3,4	V	6363	V	1,2	V	15974	V	0,2	I	252	IV
	Juncus effusus					6,2	V			0,8	IV			0,2	I		
PC	*Agrostis canina*	14,4	V	1677	V	3,2	V	219	V	1,4	V	499	V	28,0	V	2089	V
PC	*Ranunculus flammula*	0,2	V	364	V						p	21	IV	0,8	IV	48	V
PC	*Hydrocotyle vulgaris*	2,8	V	60	V					1,4	V	61	V			31	IV
CM	*Carex panicea*	30,0	V	28	V	7,6	III	5	II	17,8	V	16	V	0,6	II	33	IV
	Galium palustre	0,6	III	27	IV	1,0	IV	119	V			3	II	0,4	II	2	I
PC	*Carex oederi* ssp. *oedocarpa*	0,4	II	22	IV	0,2	I			0,4	II	7	II	0,2	I	19	IV
PC	*Carex nigra*	7,8	V	14	V	2,6	V	13	III	0,4	II	43	V	0,8	II	3	I
	Lysimachia vulgaris	1,2	III	2	I					5,2	V	92	V	8,0	V	11	III
	Molinia caerulea	7,0	V	2	I	38,0	V	37	IV	3,0	V	4	II	24,0	V	18	III
PC	*Potentilla* [*Comarum*] *palustris*	1,4	III	2	I					1,0	IV	1	I				
	Danthonia decumbens	0,2	I	6	III					0,6	III			0,2	I	2	I
PC	*Viola palustris*	0,6	III			0,2	I			0,6	III	9	II	0,2	I	1	I
	Scutellaria galericulata					1,0	V	6	III			1	I				
	Mentha aquatica agg.									0,6	III	3	I	0,2	I		
PC	*Carex echinata*									7,2	V	326	V			1	I
	Lythrum salicaria									0,4	II	117	V	0,4	II	20	IV
	Calamagrostis canescens									0,2	I	30	V	0,2	I		
	Phalaris arundinacea													0,4	II	27	IV
	Thalictrum flavum													0,2	I	1	I

Table 3. (*cont*.)

Code		Wijnjeterperschar VMC	Vfr	No.sl.	Sfr	Eexterveld VMC	Vfr	No.sl.	Sfr	Ule Krite VMC	Vfr	No.sl.	Sfr	Wyldlannen VMC	Vfr	No.sl.	Sfr
	Mostly in seed bank																
CA	*Senecio aquaticus*	e		35	V												
	Carex ovalis			31	V												
PC	*Veronica scutellata*	e		6	II												
	Myosotis scorpioides [*palustris*]	e		2	I												
	Nardus stricta	e		2	I												
	Juncus bufonius			42	V			112	V								
	Erica tetralix			3	I		e	280	V								
	Calluna vulgaris			3	I			121	V								
	Epilobium tetragonum						e	34	V								
	Stellaria media							31	V								
	Poa trivialis							30	V								
	Juncus squarrosus							23	IV								
	Conyza [*Erigeron*] *canadensis*							5	II								
	Rumex crispus							4	I								
	Plantago major ssp. *major*							3	I								
IN	*Juncus bulbosus*	e		1616	V			46	V			138	V	0,2	I	609	V
PC	*Juncus articulatus*	e		606	V		p	11	IV	0,2	I	79	V		p	30	IV
	Myosotis laxa ssp. *cespitosa*						e	135	V			1	I				
	Carex disticha											24	III				
	Eupatorium cannabinum											8	III				
PC	*Carex curta*										p	5	II				
	Carex riparia											3	II				
	Hypericum dubium											3	I				
	Typha spec.											8	III			2	I
CA	*Lychnis flos-cuculi*											1	I			8	II
	Alopecurus geniculatus											1	I			1	I

Rare species excluded from multivariate analyses detected at a single site (Vfr/Sfr: I) either in vegetation (v) (VMC=<1%) or in seed bank (s) (No.sl.<3 seeds). (See Table 1. for codes of site names.) **WTS:** CM *Carex pulicaris* v(0.2), *Galium saxatile* v(0.2), *Plantago lanceolata* v(e), *Triglochin palustris* v(e), IN *Isolepis [Scirpus] setacea* s(1), *Veronica serpyllifolia* s(1). **EXV:** *Populus tremula* v(e), *Quercus robur* v(e), *Ranunculus acris* v(e), *Taraxacum officinale* v(e), *Chenopodium album* s(2), *Cirsium arvense* s(2), *Dactylis glomerata* s(2), *Agrostis stolonifera* s(1), *Carex pilulifera* s(1), *Persicaria [Polygonum] lapathifolium* s(1). **ULE:** *Sagina procumbens* s(2), *Carex elata* s(1), *Rumex acetosella* s(1). **WYL:** *Rorippa palustris* s(1), *Solanum nigrum* s(1).

Discussion

Seed banks

Direct comparison of composition, dominance, vertical distribution and seed longevity is only possible with a limited number of German and British seed bank studies. The seed density and the number of species occurring in the seed bank decline sharply with increasing depth. This is often the case in undisturbed soil profiles (Fenner 1985). Maas & Schopp-Guth (1995), working in Bavarian fen meadows, found that the number of viable seeds in the topsoil (5 - 10 cm) was almost eight times higher than in the 20 - 30 cm soil layer. In our study we found that the seed density in the 5 - 10 cm layer was ca. 55% of that of the uppermost layer (0 - 5 cm) (WTS, EXV), while only ca. 15% was found in the 10 - 20 cm layer (ULE, WYL).

In our sites we found higher seed densities (> 25000 seed.m^{-2}) than Tallowin & Smith (1996) found in their Devon sites, although the soil volume sampled and also the number of species recorded in the seed banks were similar. Maas & Schopp-Guth (1995) used a larger sample volume of soil, but recorded a smaller number of species and much lower seed densities (500-3500.m^{-2}). As spreading of concentrated soil samples in a shallow (< 5 mm) layer promotes germination significantly (ter Heerdt et al. 1996), thick, non-concentrated sample layers in the above-mentioned experiments (spread at 3 cm and 12 cm, respectively) may have led to an underestimation of seed bank size and that of species richness to an unknown extent.
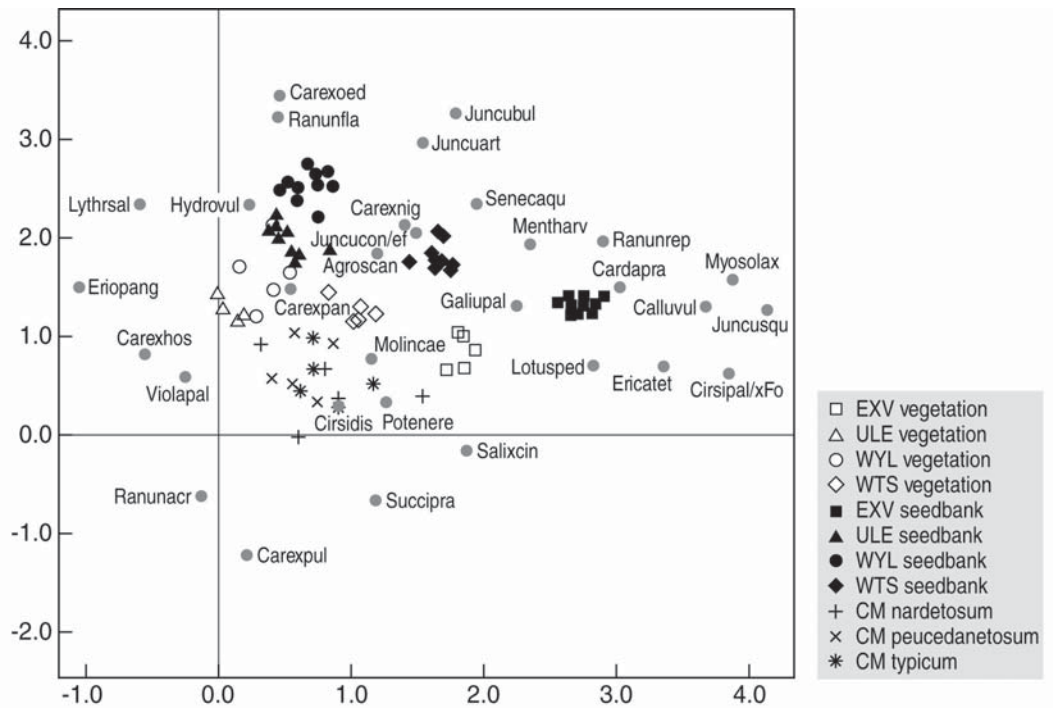
Fig. 2. Result of Detrended Correspondence Analysis; ordination of presence-absence data of (1) recent relevés (vegetation),(2) seed bank records and (3) references i.e. representative relevés of the Dutch National Vegetation Database from those subassociations of *Cirsio-Molinietum* (CM) which are still present in the study region (See Methods for selection criteria). Species frequent (>25% of sites) either in vegetation or in seed bank are shown. (See Table 1 for codes of site names.).
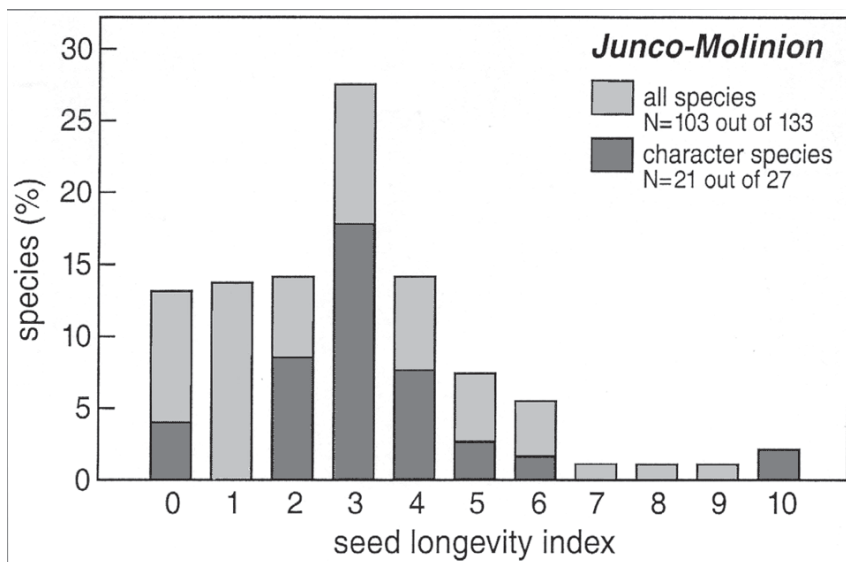
Fig. 3. Spectrum of seed longevity indices of *Junco-Molinion* species. Total number of relevés used was 336. Each species was weighted after its percentage of occurrence in the relevés. An index of 0 means transient seeds and 10 means long-term persistent seeds (Bekker et al. 1998). *n* is the number of species classified into a seed bank type from the total number of species (103 out of 133) and character species (21 out of 27) in the community, respectively.

Seed bank classification

Our findings correspond well to results published on seed banks of related plant communities (Pfadenhauer & Maas 1987; Maas & Schopp-Guth 1995; Skoglund 1990). Based on the vertical distribution of seeds in the soil (not specified in this study), most of the species had transient or short-term persistent seed banks. These findings confirm the assumption of Jansen et al. (2000) that almost all characteristic species of the *Cirsio-Molinietum* may have short-lived seed banks. *Carex panicea* and *Juncus conglomeratus* are exceptions to this rule.

The spectrum of the distribution of seed longevity indices amongst the species of the alliance *Junco-Molinion* can be constructed from the existing data of Thompson et al. (1997) combined with the new data from the present study (Fig. 3). The present study added 4 % of extra species data and 7.5 % of data on character species to the dataset, now providing data on 77% of all species belonging to this alliance (103 from 133) and also 78% of all character species (21 from 27). The longevity index for each species was calculated from at least three seed bank records, according to Bekker et al. (1998). From this spectrum we can conclude that the majority of the species has short-term persistent seeds. This holds for both the character species and the whole community.

The few long-term persistent records were especially typical in the genera *Carex* and *Juncus* (Thompson et al. 1997; Bekker et al. 1998). Our data support seed persistence in most *Carex* species but we found no seed banks of *C. hostiana* and *C. pulicaris* . This agrees with the results of Vyvey (1983) from Belgian calcareous fen meadows. In contrast, seeds of *C. hostiana* were found in soil samples from Bavarian fen meadows (Pfadenhauer & Maas 1987; Maas & Schopp-Guth 1995) whereas *C. pulicaris* was reported to have persistent seeds in a British study on *Cirsio-Molinietum* seed banks (Tallowin & Smith 1996). Based on field experiences in Dutch restoration projects both species were found within 2 - 3 yr after sod cutting (A. Jansen pers. comm.). This recent information also points to a higher seed longevity of these species. This also holds for *Viola persicifolia* that was detected in several places where it has disappeared decades before. However, the contradictory findings might also be due to sparse sampling of seed banks at Dutch and Belgian sites. The existence of sporadic persistent seed banks of apparently transient seeded species is also possible. Our method guarantees the detection of at least one seed with a 95% chance when seeds are distributed with a minimal density of 24/m^2, provided that a Poisson distribution prevails (Bakker et al. 1996; ter Heerdt et al. 1996).

The seed longevity of many species based on classification to a category of persistence may still vary considerably at the geographical scale (Thompson et al. 1997). In our study the uniformity of the seed bank classifications may reflect similarities in seed production and survival in the soil, which is probably due to the similarities of abiotic conditions and management conditions of the study sites.

Indirect evidence for seed longevity

Indirect evidence for seed longevity may be obtained in the following ways. Firstly, indications for longevity can be obtained from observing vegetation development in sod-cut areas in fen meadows (Berendse et al. 1992; Jansen & Roelofs 1996; Jansen et al. 1996; Rossenaar & Streefkerk 1997; Klooker et al. 1999; Brouwer et al. 2001). The obvious critical point of these observations is that propagules may have been imported from the vicinity. Despite this drawback, the results match fairly well with direct evidence from seed bank analyses. Sod cutting may activate long-term persistent seed banks as illustrated by early establishment of several pioneer species. Some of these species are very rare and have not been recorded in the area for a long time or were even unknown before (Jansen et al. 1996; Klooker et al. 1999). Other rare fen meadow species e.g. *Parnassia palustris*, *Cirsium dissectum*, *Succisa pratensis* and *Briza media* have only established when they had populations nearby. This is an indication that they have short-lived seed banks.

Secondly, evidence can be obtained from rare vegetation dynamical events. Grootjans et al. (1986) described a rapid spread of *Galium palustre*, *Cardamine pratensis* and *Ranunculus flammula* after rewetting of a completely deteriorated *Cirsio-Molinietum peucedanetosum* following a severe summer drought. It is not known whether seed banks of these species were activated by gap creation or whether development of vegetative organs played a role here. These species are known to make large, persistent seed banks (Thompson et al. 1997) which makes a predominant generative regeneration most likely.

Phytosociological and successional aspects

Though our results, collected in a well-defined region from similarly managed stands of a single plant community, do not allow general conclusions, many publications from Western and Central Europe also support the idea of a usually weak correlation between above-ground vegetation and below-ground seed banks (Graham & Hutchings 1988; Virágh & Gerencsér 1988; Russi et al. 1992; Csontos et al. 1996; Kirkham & Kent

1997; Halassy 2001). Also in a wider geographical and phytosociological context, this seems to be a general feature in European grasslands (Bekker et al. 1997). A likely interpretation of this discrepancy is that pioneer species with long-term persistent seed banks (Bakker 1983) are overrepresented in the seed bank. In fen meadows regeneration from the seed bank, therefore, tends to support the establishment of an initial community with several weedy species as well as some species of the *Nanocyperion* and small sedge communities *(Parvocaricetea)* instead of a rapid regeneration of the species-rich *Cirsio-Molinietum*. Such a fast colonization of *Nanocyperion* species was observed in several restoration projects (Berendse et al. 1992; Jansen & Roelofs 1996; Jansen et al. 1996; Brouwer et al. 2001). The re-establishment of *Junco-Molinion* species usually followed several years later (Jansen et al. 1996; Jansen & Roelofs 1996).

Prospects in time

The complete restoration of species-rich fen meadows (e.g. defined as at least 80% of the former characteristic species present) is only possible at recently degraded sites if measures are taken within a few years. This conclusion is in line with findings from Bavarian sites where a fast decline of seed banks of fen meadow species was assessed following an intensified agricultural use (Pfadenhauer & Maas 1987; Maas & Schopp-Guth 1995). These authors estimated that restoration activities should commence within five years after destruction of the original vegetation. Over this period incomplete stands of *Cirsio-Molinietum,* with a fast decreasing chance, can still develop, but as many characteristic species will be missing, no complete restoration seems to be possible without additional seeding. The most likely late survivors involve *Carex panicea* and *Juncus conglomeratus* as these species produce long-term persistent seeds (Vyvey & Stieperaere 1981; Vyvey 1983, 1986) that are present in the soil seed bank in large numbers (Skoglund 1990; Thompson et al. 1997; van Duren et al. 1998; Matus et al. 2001).

In most Dutch fen meadow reserves large-scale reclamation usually took place already 30 - 45 yr ago. This makes restoration of the *Cirsio-Molinietum* from soil seed banks unlikely. Consequently, the most promising sites for restoration are those where well-developed *Cirsio-Molinietum* stands still occur in the vicinity. Nevertheless, the colonization of some characteristic species and that of some *Nanocyperion* and *Parvocaricetea* species is still promising. In fen meadows surrounded by agro-industrial fields where natural propagule dispersal is limited, regular recreation of pioneer habitats by shallow sod-cutting will preserve these species and can be a sensible measure to locally renew the soil seed banks.

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