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The relationships between soil seed bank, aboveground vegetation and disturbances in old embanked marshlands of Western France

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Summary

The study deals with the influence of land use and abandonment on species composition of vegetation and seed bank in grasslands and oldfields. We wanted to explore:
(1) How the seed bank changes when agricultural practices cease? In convergence with proposals in the literature, we addressed in particular the following two questions that have been proposed by Symonides (1986), Pickett & McDonnell (1989) and Roberts & Vankat (1991) for seed bank characteristics under secondary succession: (i) Does species richness and species diversity in the soil seed bank decrease during succession? (ii) Does the density of buried seed decline during succession?
(2) What is the role played by seed bank in the recolonisation of plots disturbed by experimental disturbances?
We studied species composition of vegetation and seed bank in an experiment with grassland and oldfield plots in old embanked marshlands (called "Marais Poitevin"). In these wetlands, artificial disturbances (mowing) and natural disturbances (cattle, roebucks, coypus, voles) are very frequent. In order to mimic disturbances, experimental disturbances were generated in spring after the end of the winter flooding and emerged seedlings counted three months later. Data about the seed bank, the undisturbed vegetation and seedlings emerging in disturbed quadrats were sampled. Detrended Correspondence Analysis (DCA) of the undisturbed quadrats, disturbed quadrats and seed bank samples showed significant differences of species composition. Similarity between seed bank and undisturbed aboveground vegetation was low and not very different between grassland and oldfield. Very few seedlings emerged in the undisturbed vegetation both in grassland and oldfield, which potentially indicates the importance of gaps for seed bank expression. In Marais Poitevin, the seed bank contributed very little to the seedling flora, and vegetative regrowth clearly predominated recolonisation after disturbances. In the seed bank, few species lost after succession from grassland to oldfield vegetation were still present as seeds in the soil, but in most cases species lost were not recorded in the seed bank. The results have shown that species richness and species diversity in the seed bank decrease during succession. On the other hand, the density of buried seeds did not decrease significantly from grassland to oldfield.

Key words: grassland, meadow, succession, diversity, abandonment of farming.

1. Introduction

The soil seed bank plays an important role in the composition of different plant communities and especially in their conservation (Grubb 1977; Wisheu & Keddy 1991). Grassland seed banks and their relationships to vegetation had been the subject of much recent attention (Peco et al. 1998). The understanding of the potential of a seed bank to alter grassland composition (Rice 1989), its potential for restoring species-rich

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pastures (McDonald et al. 1996) and maintaining floristic diversity (Bakker et al. 1991; Willems et al. 1993) are some of the reasons that have motivated researchers to compare the composition of the above-ground vegetation with seed reserves hidden in the soil. The seed bank is a major functional compartment of a plant community (Templeton & Levin 1979), in that its role as a "storage compartment" (*sensu* Chesson 1983) allows population maintenance according to changes in reproduction performances either between years or between sites. Thompson & Grime (1979) defined four types of seed banks among the most common species in temperate regions, characterised by singularities in the persistence of their seeds in soil. These types range from transient seed banks constituted by seeds that germinate in greater numbers immediately after dispersal, to persistent seed banks with seeds that remain dormant in the soil over a longer period (more than 1 year) – see also Hölzel & Otte (2004).

Most studies of grasslands dominated by perennial grasses have found low similarities between the seed bank and the vegetation (Milberg 1995; Bakker et al. 1996; Peco et al. 1998; Edwards & Crawley 1999). These discrepancies have been explained by the minor contribution of the dominant perennial meadow species to the formation of seed banks. These species generally have a low seed production because they alternate sexual reproduction with vegetative forms (Champness & Morris 1948) and their seeds have a short-term persistence in the soil (Bakker 1989; Thompson 1992). Moreover, where important seed banks exist in such perennial grasslands, the soil seed banks often contain large numbers of seeds of annual ruderal species (Zimmergren 1980) that reduce the similarity between the vegetation and the seed bank. This is a good illustration of the fact that seeds of the later type of species can survive for many decades, even centuries, in the soil (Bakker 1989; Milberg 1992). It also indicates that these species could reappear from the seed bank if these grasslands were to be ploughed again. Consequently, their presence in the seed bank can greatly influence the species composition after a disturbance (Vankat & Carson 1991).

Also, exceptions from the normally weak similarity between seed bank and vegetation have been found. They have been described from similar findings in freshwater tidal marshes (Leck & Graveline 1979), in annual Mediterranean pastures (Maranon & Bartolome 1989; Levassor et al. 1991) and in a desert short grass community in New Mexico (Henderson et al. 1988). These results have been linked to the fact that these systems are subject to a regime of frequent and unpredictable disturbances either by flooding in the case of the tidal marsh or by drought in the other two types of grasslands (Levassor et al. 1991). The common denominator of these disturbed areas is the predominance of annual species (Peco et al. 1998). Some authors (Van Der Valk 1992; Grillas et al. 1993) suggested that the seed bank is the major source of seedling recruitment after disturbances in grasslands. This is a crucial role generally played by seed banks in ecosystems where disturbances do not allow plants to reproduce each year (Moore 1980; Henderson et al. 1988). However, it should be noted that revegetation after disturbances in perennial grasslands is often dominated by regrowth from vegetative parts rather than by seedlings (Milberg 1993). Although seed banks have been studied in many types of habitats (Leck & Graveline 1979), their exact functioning remains rather poorly known (Grime 1979), particularly in wetlands.

We studied seed banks and experimental disturbances in an experiment with farmed and abandoned grassland (oldfield) vegetation located in old embanked marshlands in western France characterised by two contrasting vegetation types which are determined by local land uses (farming *versus* land abandonment). We wanted to explore:

(1) How the seed bank changes when agricultural practices cease? Here, we addressed the two following questions that have been proposed by Symonides (1986), Pickett & Mcdonnell (1989), Roberts & Vankat (1991) for seed bank characteristics under secondary succession: (i) Does the density of buried seeds decline during succession? (ii) Does species richness and species diversity in the soil seed bank decrease during succession?
(2) What is the role played by seed bank in the recolonisation of quadrats disturbed by experimental disturbances?

2. Materials and Methods

2.1. Study site

The sampling area was located in wetlands called "Marais Poitevin" (46°30'–46°27' North and 1°30'– 1°35' West), the largest area of marsh wetlands on the French Atlantic coast (120.000 ha) (Fig. 1). These wetlands are old embanked marshlands. The climate is a warm Atlantic type with a mean annual rainfall of 655 mm (Météo France data). The mean monthly minimum temperature is 6.6 °C and the mean monthly maximum temperature is 16.9 °C. The Marais Poitevin is a wetland of international importance for wildlife since it is situated along one of the main bird migration corridors. Extensive drainage has taken place in the last decade in order to allow cereal grain cultivation, but natural wet meadows, especially common grazing lands, still survive. Grazing by cattle and horses is traditionally practised from the end of April to the end of December each year. Experiments were conducted on one of these commons.

The soils can be classified as reductisols in the wet depressions and as sodisols on the higher levels (AFES 1992). The vegetation has been described in detail by Bouzille (1992). The experiments were conducted in two different flooded fields. In the regularly grazed grassland, hygrophytic species such as G*lyceria fluitans*, *Oenanthe fistulosa*, *Eleocharis palustris*, and *Agrostis stolonifera* occur in wet depressions. The higher levels are mainly covered with grasses such as *Cynosurus cristatus*, *Gaudinia fragilis*, *Bromus commutatus* and *Lolium perenne.* The oldfield which was abandoned since 3 years is dominated by two competitive species: *Agrostis stolonifera* in the wet depressions and *Elymus repens* in the higher levels.

2.2. Experimental disturbances and vegetation data

Two experimental sampling plots (10 m × 10 m) were selected both in grassland and oldfield in a homogeneous area to avoid edge effects. Within each plot, 15 quadrats were randomly distributed. Size of the quadrats was 0.25 m^2 (0.5 m × 0.5 m) (Amiaud 1998). In each plot, experimental disturbances were created in spring (March 1996) in the quadrats devoted to disturbances (10 quadrats: 5 in grassland and 5 in oldfield). Fives replicates were assumed to be sufficient due to homogeneous vegetation. The above-ground living vegetation, litter and all dead plant material were removed (but not killed). In each sampling plot, 5 undisturbed quadrats (labelled "Controls") were also surveyed.

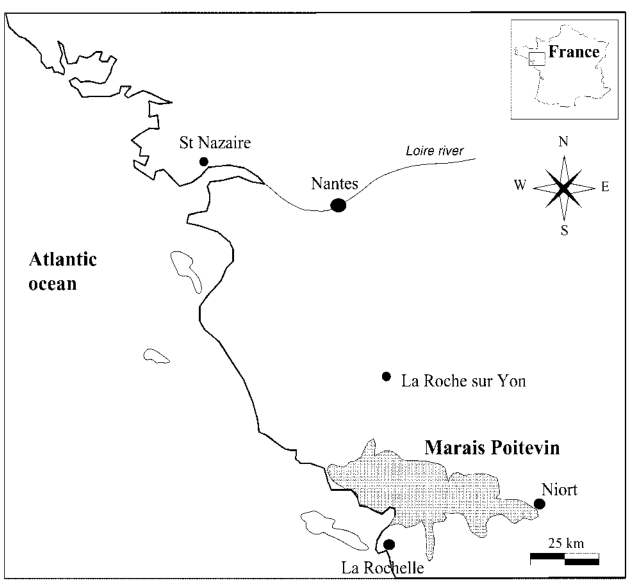

Fig. 1 Geographic location of the Marais Poitevin (46°30'–46°27' North, 1°30'–1°35' West).

The vegetation sampling was performed during summer (July 1996) when the development of plants was in its optimum. Floristic information was obtained by surveys carried out once in each quadrat. The cover of each taxon was estimated, using the cover scale of Braun-Blanquet (Westhoff & Van Der Maarel 1978): (1) cover < 5%; (2) 5% < cover < 25%; (3) 25% < cover < 50%; (4) 50% < cover < 75%; (5) cover > 75%. The code "+" was used for species represented only by a few individuals. The nomenclature of Flora Europaea (Tutin et al. 1964–1980) was used.

2.3. Seed bank sampling

The seed bank was sampled in March 1996. This date, after the germination period but before new seed dispersal for most species, was chosen to assess the persistent part of the seed bank (according to Thompson & Grime 1979). We used the method developed by Lavorel et al. (1993) consisting of a randomly sampling within each sampling plot. 10 soil samples were collected (5 per sampling plot: 5 in grassland, 5 in oldfield). Soil samples were taken with a metal square (10 cm × 10 cm) in the centre of each quadrat devoted to seed bank sampling. The majority of viable seeds is normally concentrated in the very first centimetres of the ground (Lavorel et al. 1993; Bonis & Lepart 1994). The depth of sampling was 5 cm. The soil samples were sorted to eliminate plant fragments and stones. Soil samples were placed in a cold greenhouse and kept moist. Depth of the soil layer in the germination trays was 2 cm. Seedling identifications were made using seedling floras (Hanf 1976; Hubbard 1984). Emerging seedlings were identified and removed or replanted for later identification. In order to favour the maximum of germination, after identification, seedlings were pulled out to maintain a weak density in the germination trays and to allow the germination of other seeds. At the end of the first two months of the experiments, the soil samples were carefully turned over in order to facilitate the emergence of new seedlings (Roberts 1981). After five months, sampling was stopped as no more seedlings occurred for several consecutive weeks. To sample the seed dispersion of exogenous species inside the greenhouse, several samples containing sterile soil were set up additionally.

2.4. Data analyses

To compare the composition and abundance of species in the vegetation (undisturbed quadrats and disturbed quadrats) and in the seed bank samples, a multivariate ordination was conducted using Detrended Correspondence Analysis (DCA) (Hill 1979; Hill & Gauch 1980). DCA was used to examine variation in plant species composition and was applied to the species frequency data. DCA was chosen in preference to Correspondence Analysis (CA) because the latter showed an arch effect in the plane of axes 1 and 2 (Jongman et al. 1987). All analyses were performed using CANOCO version 3.12 (Ter Braak 1991), following the default options for DCA. Graphical plots of data ordinations were constructed using CANODRAW (Smilauer 1992), using the DECORANA program, with no down weighting of rare species and with a log (x+1) transformation of the data to match up the data. Using DCA simultaneous ordinations of vegetation quadrats, seed bank samples and species were obtained.

For vegetation data, the sampling method used the cover scale of Braun-Blanquet (Westhoff & Van Der Maarel 1978) but, because of the non-linear nature of this scale, it was necessary to convert it into cover percentages for the statistical analysis using the median value of cover. We used: 0.05 for the class (1) cover < 5%; 0.15 for the class (2) 5% < cover < 25%; 0.375 for the class (3) 25% < cover < 50%; 0.625 for the class (4) 50% < cover < 75%; 0.875 for the class (5) cover > 75%. For the class "+", we used the frequency 0.0125. The total cover obtained for one quadrat can exceed 100% because the vegetation can occupy several strata over the same ground area. For seed bank data, species frequencies were calculated as the number of seedlings of one species divided by the total number of seedlings in the seed bank per soil sample. Our data set finally consisted of one statistical matrix: the 'samples-species' matrix Y, with species frequency data for the p = 39 species (columns) in the n = 30 samples (rows).

For each undisturbed quadrat, disturbed quadrat and seed bank sample, the diversity, using the SHANNON index (Westhoff & Van Der Maarel 1978) and species richness was determined. We calculated the mean species richness (S), the mean species diversity (H'a) from all the quadrats of a same treatment. Species richness and species diversity were compared by means of a one-way analysis of variance between collecting stations for each type of quadrats. They were also compared with respect to the three treatments for each collecting station. Analyses of variance were conducted with Statgraphics Plus Software (version 2.1, 1995) using Tukey's test (Sokal & Rohlf 1981).

JACCARD's similarity coefficient (Westhoff & Van Der Maarel 1978) was calculated as the number of species observed both in the seed bank and aboveground vegetation (undisturbed or disturbed vegetation) divided by the total number of species in the seed bank and aboveground vegetation on a per sample basis.

3. Results

3.1. Floristic composition of undisturbed, disturbed areas and seed bank samples

DCA of the matrix Y estimated a total variance of species composition among the quadrats of 1.98 (Table 1). The first two axes had contributions greater than 10% and were significant for interpretations (Lavorel et al. 1998). Axis 1 of the DCA (Fig. 2) separated undisturbed quadrats in grassland from seed bank samples (grassland and oldfield). The first group (A), which was composed of 5 quadrats, was characterised by grassland species *(Alopecurus bulbosus, Juncus gerardi, Hordeum secalinum …)*. The second group (B) contained 10 quadrats and was composed by species that do not exist in the aboveground vegetation *(Anagallis arvensis, Trifolium fragiferum, Chamomilla recutita …)*. Axis 2 separated 5 undisturbed quadrats in the oldfield from 10 disturbed quadrats (grassland and oldfield). The third group (C) was composed by oldfield species *(Agrostis stolonifera, Elymus repens …)*. The last group (D) was characterised by species that were common to the seed bank samples and the undisturbed quadrats (*Ranunculus sardous, Poa trivialis* …).

3.2. Similarity between seed bank and aboveground vegetation

Overall, the similarity between the different treatments (controls, disturbed quadrats and seed bank samples) ranged between 6% and 72% (Table 2). The similarity between the controls and the seed bank for each vegetation type was relatively low, with values ranging from 22% to 29%. This similarity tended to decrease when the successional stage increased (29% in grassland to 22% in oldfield).

Varying similarities were observed when seed bank samples were compared to disturbed quadrats. In this case, the similarity was 18% in grassland and 6% in oldfield.

The confrontation between controls and disturbed quadrats revealed a strong similarity in grassland (58%) and a low similarity in oldfield (8%).

Similarity between grassland seed bank and oldfield seed bank was high (72%).

Table 1. Results of the multivariate analyses. Detrended Correspondence Analysis (DCA) of species composition.

Analysis	Factor *i*	Eigenvalue I_i	% inertia
DCA – Marais Poitevin	1	0.536	27.0
	2	0.252	12.7
Y: 39 species × 30 quadrats	3	0.101	5.1
	$\lambda_1 = \Sigma\lambda_i = 1.98$		

Table 2. Jaccard similarity coefficients (%) between treatments for each vegetation type. 'Gra': Grassland – 'Old': Oldfield – 'C': Controls – 'Dist': Disturbances – 'SB': Seed bank.

Treatments	Gra-C	Gra-Dist	Gra-SB	Old-C	Old-Dist	Old-SB
Gra-C	100					
Gra-Dist	58	100				
Gra-SB	29	18	100			
Old-C	57	38	26	100		
Old-Dist	12	9	12	8	100	
Old-SB	21	20	72	22	6	100

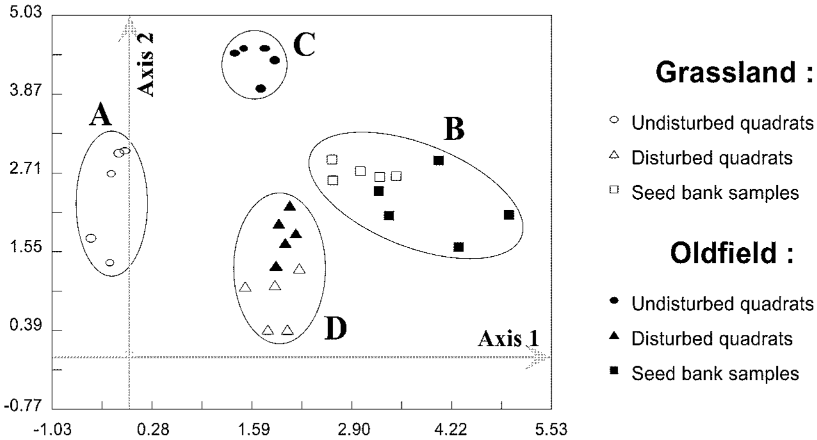

Fig. 2 Detrended Correspondence Analysis (DCA) of species composition in the 30 quadrats. Four species assemblages ("A" to "D") were identified by overlaying the projections of quadrats and species in the plane formed by the first two axes of the analysis (Filled symbols: oldfield – Open symbols: grassland).

3.3. Seed banks

The five months germination period revealed a total of 2558 seedlings (1367 in grassland, 1191 in oldfield) representing 29 species (27 species in grassland; 23 species in oldfield) (Table 3). The total seedling density was between 27340 seedlings/m^2 in grassland and 23820 seedlings/m^2 in oldfield. The difference in seedling density was not significant between grassland and oldfield ($F(1, 9) = 0.59$, $p = 0.46$). A small number of species caused a great number of germinations both in grassland and in oldfield. Half of the germinations came from 5 species (out of 29): *Ranunculus sardous* (12%), *Trifolium ornithopodioides* (11 %), *Trifolium squamosum* (11 %), *Chamomilla recutita* (10 %) and *Trifolium fragiferum* (9 %). A comparison between grassland and oldfield showed that 5 species (*Alopecurus bulbosus*, *Cynosurus cristatus*, *Juncus gerardi*, *Lolium perenne*, *Trifolium ornithopodioides*) were recorded only in the undisturbed quadrats of the grassland, and 4 species (*Cardamine hirsuta*, *Cirsium vulgare*, *Oenanthe silaifolia*, *Trifolium subterraneum*) were found only in undisturbed quadrats of the oldfield.

3.4. Variation in species richness and diversity in seed banks, disturbed and undisturbed vegetation

In controls, species richness was higher in grassland (11.80) than in oldfield (11.20) (Table 4). The differences in species richness between grassland and oldfield were not significant ($F(1,9) = 0.46$, $p = 0.52$). Neither significant differences in diversity were observed between grassland and oldfield ($F(1,9) = 1.52$, $p = 0.25$). In seed bank samples, the analysis of variance showed significant differences between grassland and oldfield in both species richness ($F(1,9) = 14.70$, $p < 0.01$) and species diversity ($F(1,9) = 7.02$, $p < 0.05$). In disturbed quadrats, no significant differences were observed between grassland and oldfield, neither in species richness ($F(1,9) = 0.14$, $p = 0.72$) nor in species diversity ($F(1,9) = 2.05$, $p < 0.19$).

4. Discussion

4.1. Seed bank and aboveground vegetation similarity

Like most studies of perennial grasslands (Milberg 1992; Poschlod & Jackel 1993; Eriksson & Eriksson 1997; Peco et al. 1998) or salt marshes (Egan & Ungar 2000), we found a lack of correspondence between the species composition of the seed bank and the undisturbed aboveground vegetation. This discrepancy was slightly higher in oldfield (22%) than in grassland (29%). The weak similarity between vegetation and seed bank was attributed to the great proportion of species that were absent from the vegetation and whose seeds have a significant viability in the ground based on their strategies of opportunistic species. In oldfield such seed banks still contained species of previous successional stages which were mostly grassland perennial species *(Trifolium fragiferum, Agrostis stolonifera, Lolium perenne, Cynosurus cristatus)*. In grassland, species of previous successional stages in the seed bank samples were mostly annual ruderal species (species 'R' *sensu* Grime 1979) *(Ranunculus sardous, Trifolium ornithopodioides)*. These results from wetland plant communities support conclusions drawn in other grassland studies (Van Der Valk & Davis 1976; Kiirikki 1993) where seed banks also contained seeds of species which disappeared in the aboveground vegetation in early successional stages. One reason for the presence of species of earlier successional stages in the seed banks can be the suppression of seedling emergence by litter. This is most important in oldfields where the litter layer is thick (Facelli & Facelli 1993; Jensen 1998), which leads to a conservation of seeds in the soil. In oldfield, litter can reach weights of up to 600 g/m^2 and thickness up to 5 cm or 10 cm (Amiaud 1998). Another explana-

Table 3. Frequency (%) (with standard deviations +/-) of taxa. Data from 5 replicates have been lumped. Frequencies in the undisturbed and disturbed vegetation are based on presence in quadrats and frequencies in the seed bank are based on presence in soil samples. Life history: annual (A) and perennial (P) species. Numbers within parentheses are number of seedlings recorded.

			Marais Poitevin					
			Grassland			**Oldfield**		
			Undisturbed quadrats (Controls)	**Disturbed quadrats**	**Seed bank samples**	**Undisturbed quadrats (Controls)**	**Disturbed quadrats**	**Seed bank samples**
Species recorded only in the grassland	**Species code**	**Life history**						
Alopecurus bulbosus	Abul	P	11.75 (+/–6.93)	4.25 (+/–5.12)			1.25 (+/–0.00)	
Cynosurus cristatus	Ccri	P	0.25 (+/–0.00)		0.51 (+/–0.35) (7)			2.77 (+/–1.73) (33)
Juncus gerardi	Jger	P	14.50 (+/–8.71)		0.07 (+/–0.00) (1)			
Lolium perenne	Lper	P	4.25 (+/–3.78)	1.25 (+/–1.66	9.80 (+/–2.72) (134)		5.00 (+/–2.34)	4.03 (+/–2.25) (48)
Trifolium ornithopodiodes	Torn	A	1.50 (+/–1.53)	6.75 (+/–4.37)	16.09 (+/–4.50) (220)		0.94 (+/–0.44)	4.37 (+/–5.70) (52)
Species recorded only in the oldfield								
Cardamine hirsuta	Chir	A			4.02 (+/–1.03) (55)	10.00 (+/–6.80)	1.25 (+/–0.00)	8.98 (+/–2.22) (107)
Cirsium vulgare	Cvul	P			0.37 (+/–0.23) (5)	0.50 (+/–0.02)		0.08 (+/–0.00) (1)
Oenanthe silaifolia	Osil	P				0.25 (+/–0.00)	0.31 (+/–0.00)	
Trifolium subterraneum	Tsub	A			0.22 (+/–0.00) (3)	0.50 (+/–0.05)	0.31 (+/–0.00)	0.08 (+/–0.00) (1)
Species recorded only in the seed bank								
Anagalis arvensis	Aarv	A			9.14 (+/–2.41) (125)			2.02 (+/–1.00) (24)
Buplerum tenuissinum	Bten	A			0.07 (+/–0.00) (1)			
Chamaemelum nobile	Cnob	P			2.41 (+/–1.27) (33)			6.55 (+/–8.92) (78)
Chamomilla recutita	Crec	A			5.56 (+/–3.22) (76)			15.79 (+/–4.74) (188)
Chenopodium album	Calb	A			0.51 (+/–0.34) (7)			8.14 (+/–3.80) (97)
Eleocharis palustris	Epal	P			0.07 (+/–0.00) (1)			0.17 (+/–0.00) (2)
Epilobium hirsutum	Ehir	P			0.07 (+/–0.00) (1)			
Rumex crispus	Rcri	P			1.46 (+/–1.01) (20)			
Senecio vulgaris	Svul	A			0.51 (+/–0.34) (7)			0.42 (+/–0.28) (5)
Sonchus asper	Sasp	A			0.95 (+/–0.64) (13)			1.01 (+/–0.62) (12)
Trifolium repens	Trep	P			0.73 (+/–0.23) (10)			0.50 (+/–0.25) (6)
Trifolium elegans	Tele	P						0.08 (+/–0.00) (1)
Trifolium fragiferum	Tfra	P			7.24 (+/–3.77) (99)			11.17 (+/–4.72) (133)
Trifolium pratense	Tpra	P			4.32 (+/–0.65) (59)			2.43 (+/–0.84) (29)
Trifolium resupinatum	Tres	A			1.54 (+/–0.67) (21)			0.34 (+/–0.34) (4)
Other species								
Carex divisa	Cdiv	P	11.00 (+/–2.51)			5.00 (+/–0.29)		
Cerastium glomeratum	Cglo	P	2.50 (+/–1.48)	0.25 (+/–0.00)		1.25 (+/–0.07)		

Table 3. (continued)

			Marais Poitevin					
			Grassland			Oldfield		
			Undisturbed quadrats (Controls)	Disturbed quadrats	Seed bank samples	Undisturbed quadrats (Controls)	Disturbed quadrats	Seed bank samples
Other species								
Draba verna	Dver	P	3.50 (+/–1.29)	0.50 (+/–0.38)		3.25 (+/–1.08)	4.63 (+/–1.46)	
Elymus repens	Erep	P	8.25 (+/–2.84)			33.00 (+/–5.04)	1.25 (+/–0.00)	
Hordeum secalinum	Hsec	P	5.25 (+/–3.41)	1.25 (+/–0.93)		0.25 (+/–0.00)	0.31 (+/–0.00)	
Myosotis discolor	Mdis	P		0.50 (+/–0.38)				
Poa annua	Pann	P	0.75 (+/–0.11)	2.00 (+/–0.01)		0.75 (+/–0.08)	1.56 (+/–1.55)	
Agrostis stolonifera	Asto	P	1.00 (+/–0.00)		6.07 (+/–1.78) (83)	8.25 (+/–3.36)	0.31 (+/–0.00)	4.70 (+/–0.84) (56)
Bromus commutatus	Bcom	A	10.00 (+/–3.70)	8.25 (+/–3.19)	0.07 (+/–0.00) (1)	0.50 (+/–0.01)	0.31 (+/–0.00)	0.34 (+/–0.06) (4)
Geranium dissectum	Gdis	A	0.25 (+/–0.00)		0.29 (+/–0.17) (4)	4.25 (+/–0.79)		
Poa trivialis	Ptri	P	0.25 (+/–0.00)	13.00 (+/–2.50)	2.85 (+/–0.59) (39)	0.25 (+/–0.00)	32.50 (+/–7.69)	3.95 (+/–2.31) (47)
Ranunculus repens	Rrep	P		6.00 (+/–1.80)				0.34 (+/–0.00) (4)
Ranunculus sardous	Rsar	A	10.00 (+/–3.70)	33.00 (+/–11.43)	3.95 (+/–0.95) (54)	19.50 (+/–5.29)	43.75 (+/–14.48)	21.75 (+/–8.45) (259)
Trifolium squamosum	Tsqu	A	7.00 (+/–2.87)	1.50 (+/–1.51)	21.07 (+/–4.89) (288)	15.50 (+/–6.02)	0.63 (+/–0.02)	

tion of the weak similarity between vegetation and seed bank could come from species, which were only present in the vegetation but absent in the seed bank. We found such species that are perennial and rely almost exclusively on vegetative reproduction *(Alopecurus bulbosus, Carex divisa, Elymus repens, Oenanthe silaifolia)*. They greatly contribute to decrease the similarity between seed bank and vegetation cover. Such species have been described as the disporum type, i.e., species that show no evidence of forming a seed bank (Thompson 1992). In addition, some species *(Cerastium glomeratum, Elymus repens, Poa annua)* identified as having a persistent seed bank by Grime et al. (1988) did not always recover from the seed bank. Some species *(Juncus gerardi, Eleocharis palustris)* were identified only one or two times in the seed bank. Possibly, they may have escaped sometimes from the detection. Such a difficulty of recording rare species in the soil samples was also mentioned by Peco et al. (1998). This may have increased additionally the dissimilarity between vegetation and the documented seed bank (Edward & Crawley 1999).

4.2. Seed bank and land abandonment relationships

4.2.1. Similarity

In the Marais Poitevin, the similarity between seed banks in grassland and in oldfield was great (72%). In contrast, another study in similar floodplain communities (Touzard et al. 2002) has shown a weak similarity (40%) between grassland seed bank and oldfield seed bank. Seeds of many grasslands species are short-lived. Therefore, only few species can be recruited from the seed bank when grassland vegetation abandoned for several years is restored (Doneland & Thompson 1980; Bakker & Berendse 1999). Sometimes, few

Table 4. Species richness (S) and species diversity (H'α) in the controls, disturbed quadrats, seed bank samples in grassland and oldfield.

Parameters	Treatments	Marais Poitevin	
		Grassland	Oldfield
Species richness (S)	Controls	11.80 (+/–1.30)	11.20 (+/–1.48)
	Disturbances	7.80 (+/–2.28)	7.25 (+/–2.06)
	Seed bank	18.00 (+(–1.00)	15.40 (+/–1.14)
Species diversity (H'α)	Controls	2.84 (+/–0.36)	2.61 (+/–0.24
	Disturbances	2.02 (+/–0.28)	1.72 (+/–0.35)
	Seed bank	3.41 (+/–0.19)	3.08 (+/–0.20)

species colonising the grassland can be still detected in the seed bank of the oldfield. But in most cases, the lost species (in vegetation and seed banks) of earlier successional stages could not be detected in the seed bank of the abandoned areas (Milberg 1995). Our results showed that some grassland species *(Trifolium ornithopodioides, Cynosurus cristatus, Lolium perenne)* were still found in the seed bank of the oldfield, probably because abandonment of the land occurred only three years before. Likewise, investigating the seed bank of abandoned fields in Southern Finland, Kiirikki (1993) found that, even after a period of abandonment of 21 years, the seed bank was still dominated by species common in the early stages of secondary succession.

4.2.2. Species diversity

The hypothesis that species richness or species diversity in the seed bank decreases during succession has been proposed both for grasslands (Doneland & Thompson 1980) and oldfields (Symonides 1986; Roberts & Vankat 1991). Our analysis confirmed this assumption. The changes may be explained by a decrease of seed production of the plants and of seeds longevity in the ground or by an increase of seed predation in old successional stages (Roberts & Vankat 1991). In contrast to these findings, Milberg (1995) noted a constant number of species from grassland to oldfield in wet herbaceous systems.

4.2.3. Density of seeds

The density of buried seeds has been postulated to decline during succession from grasslands to oldfields (Symonides 1986; Pickett & Mcdonnell 1989; Roberts & Vankat 1991). In the Marais Poitevin, seed density did not decrease significantly from grassland to oldfield. Several interpretations could be proposed to explain why seed abundance in the soil need not necessarily decrease during grassland succession following cessation of land uses: (1) In mown areas, a substantial part of the seeds produced are eaten by the grazing animals or exported by mowing, as observed also in the Marais Poitevin. In addition, the seed bank accumulation rate is a function of the rate of seed burial in the soil. McDonald et al. (1996) stated that grazing allows the incorporation of seeds deeply in the soil, where light could not penetrate. This may prevent seeds from germination, and hence enlarge the seed bank. In the present study, the soil was much less compact in oldfield that in grassland. Consequently, more seeds may have been buried actively in oldfield, especially by earthworms (Grant 1983; Van Tooren 1988). (2) Moreover, only few species often made up 80–90% of the seed bank *(Ranunculus sardous, Trifolium ornithopodioides, Trifolium squamosum, Chamomilla recutita* and *Trifolium fragiferum)*. Hence, seed density to a very large extent can depend on the distribution and seed production of such dominant species.

The seed density values observed in the Marais Poitevin were relatively high in comparison with those observed in some grazed and mown German meadows (Poschlod 1993) with 4000 seeds/m^2 or in some English meadows (McDonald et al. 1996) with 3376 seeds/m^2. Other authors (e.g. Kiirikki 1993) found even greater seedling densities (between 35000 and 55000 seed/m^2) in wet grassland communities. Rich seed banks are often observed in regularly disturbed areas below wet meadows exposed to flooding (Van Der Valk & Davis 1979; Thompson 1992).

4.3. Seed bank expression and disturbances

The literature on gap regeneration in plant communities in relation to disturbance type, time, size and frequency is extensive (Rapp & Rabinowitz 1985; Bullock et al. 1994; Lavorel et al. 1998; Edwards & Crawley 1999). Many of these authors showed the seeds reserves hidden in the soil germinate when natural or human disturbances took place. In Marais Poitevin, the results of the study did not confirm such a pattern. In fact, despite the high density of seeds in the soil (as shown by seed bank sampling) and the large size of disturbed areas, few seedlings were found recovered from the seed bank in the disturbed vegetation of the two plots (grassland and oldfield). Most of the taxa seeds of which were detected in the seed bank were not found as seedlings in the quadrats after experimental disturbances. Rather, plant recolonisation in the disturbed areas was dominated by the way of vegetative reproduction of species. This could have been resulted in part from the compaction of the soil due to grazing in spring during wet conditions, which prevented seedling emergence from the seeds after disturbances. In our experimental approach, we removed the perennial vegetation but did not enough disturb the soil surface or mix the soil profile, as it might occur with natural disturbances such as grazing and trampling by mammals. Consequently, the specific conditions required for seedling emergence may not have been met. In a similar experiment, Milberg (1993) found no obvious correspondence between seed bank and the emerging seedlings in a wet grassland in central Sweden. Further, the predominance of perennial species in the undisturbed vegetation possibly reduced the abundance of natural gaps and the probabilities of seedling establishment. Thus many species may remain in the seed bank and maintain the below ground potential species composition for at least the first years after mowing or grazing have ceased. Hence, although seed banks of both grassland and oldfield were potentially rich in species, they contributed little to the species richness or diversity of the standing vegetation.

There might be still another explanation for the negligible recruitment of seedlings from the seed bank into our experimentally created gaps in Marais Poitevin: The timing of the disturbance relative to the availability of seeds capable of germination may have been an other important factor (Lavorel et al. 1994; Kotanen 1996; Edwards & Crawley 1999). Even if dormancy was broken by gap opening, the time for germination (late spring) may have been inadequate for a successful plant establishment (certainly for all autumn germinators).

In another study (Touzard et al. 2002), a significant recruitment from the seed bank into the experimentally created gaps was observed. The species that recolonised disturbed areas were present in the seed bank and this could have been the reason for the high similarity between seed bank and disturbed areas found there (more than 50% in some disturbances quadrats). These latter findings agree with results of Chambers (1993) in alpine meadows and of Lavorel et al. (1993) in Mediterranean oldfields who showed that the similarity between the disturbed areas and the seed bank could be very high (about 70%).

Plant species can potentially use the sexual or the vegetative way to colonise disturbed areas and both is possible also, in Marais Poitevin. However, it appears that the vegetative form is the more effective way of recolonisation used by the species of the vegetation that prevails there. These taxa probably allocate distinctly more resources towards the vegetative reproduction. To verify this, an analysis will follow comparing the efficiency of the sexual reproduction of the most important species of this vegetation, quantifying in particular seed production, seed dissemination, germinative capacities of the seeds, on the hand, and the capacity for clonal attributes, fragmentation abilities on the other hand.

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