Plant Ecology **174:** 279–291, 2004.

Inter-annual variation in the soil seed bank of flood-meadows over two years with different flooding patterns

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Received 20 November 2002; accepted in revised form 12 September 2003

Key words: Disturbance, DCA-ordination, Dormancy cycles, Mantel test, Recruitment, Upper Rhine, Flooding variation

Abstract

Persistent soil seed banks are presumed to play a significant role in bridging and exploiting the effects of major flood disturbances in riparian systems. However, presently there is little empirical data on the correlation between flooding and seed bank dynamics. The objective of this study was to assess the impact of inter-annual flooding variation on soil seed bank dynamics in flood-meadows. We analysed seed bank composition at 46 plots along the northern Upper Rhine River, Germany, after two periods with contrasting flooding conditions (1996-1997: low and rare flooding; 1998-1999 high and very frequent flooding). Between both sampling occasions the total number of seedlings emerging from the seed bank decreased by 50% and average species-richness per sample by 30%, irrespective of the sampling depth. Similar decline occurred in mesophytes and wetland species as well as over different functional groups, with the exception of legumes. Considerable compositional changes in the seed bank were also indicated by shifts in DCA ordination and by the comparison of similarity matrices from both years with the Mantel test. The Mantel test also confirmed that compositional changes were more pronounced in the seed bank than in aboveground vegetation. There was poor correlation between the decline in total seed densities and species in the soil seed bank and environmental variables such as flooding duration and ecological groupings such as floodplain compartment and seed bank community types. Further distinct patterns of decline and persistence were evident only at the species level. While 21 species displayed a significant decline, only two species increased. Annual arable weeds and perennial ruderals with high temperature or nutrient requirements to break dark dormancy were amongst the most significantly declining species. In contrast, there was no decline in typical winter annuals and certain perennials that preferably germinate in autumn and fall into dormancy at the beginning of the warm period. Generally, differences in germination requirements and dormancy cycles of species gave the best explanation for the patterns of decline and persistence after intense flooding. Given these findings, the heavy depletion of the persistent soil seed bank we observed is most likely attributed to a post-flood germination flush due to very favourable recruitment conditions prevailing during the draw-down period after early summer flooding in 1999. The results of our study suggest that persistent soil seed banks are of outstanding importance to bridge and exploit the highly variable hydrological conditions that are typical of flood-meadows. Thus, they play a significant role in maintaining the floristic diversity of this habitat type over time and space.

Introduction

Flooding dynamics are of major importance in structuring vegetation and plant diversity along riparian systems. While such flood induced dynamics in aboveground vegetation have been studied previously (e.g., Balátová-Tuláčková 1979; Vervuren et al. 2003), little is known about the effects of floods on the size and composition of soil seed banks and their potential role in regeneration after such major disturbances. As emphasized in a recent review by Goodson et al. (2001), there are generally enormous research gaps relating to interactions between fluvial processes and riparian seed banks. Regeneration from the persistent soil seed bank was found to be an important and even dominant process in succession after draw down and rewetting in temporary wetlands (e.g., van der Valk and Davis 1978; van der Valk 1981; Casanova and Brock 2000) as well as in disturbance driven tidal freshwater and salt marshes (e.g., Parker and Leck 1985; Baldwin et al. 1996; Bekker et al. 1999; Jutila 2001). Thus, we presumed that soil seed banks might play a comparable role in riparian grasslands, which are also subject to irregular und unpredictable flood disturbances.

In a previous study (Hölzel and Otte 2001) we analysed the impact of fluvial input on the composition of soil seed banks in flood-meadows by the comparison of different hydrological floodplain compartments that differ with respect to their connectivity to the river system. The focus of the present paper will be on the inter-annual variation in soil seed banks of flood-meadows over two years with contrasting flooding conditions prior to sampling.

Effects of inundation on soil seed banks are usually examined in factorial experiments that simulate flooding by the submergence of soil samples under artificial laboratory conditions. Most of these studies revealed a clear inhibition in germination of many semi-terrestrial and terrestrial species by constant inundation, while only the emergence of certain aquatic species was significantly facilitated (van der Valk and Davis 1978; Gerritsen and Greening 1989; Finlayson et al. 1990; Seabloom et al. 1998; Abernethy and Willby 1999; Boedeltje et al. 2002; Nicol et al. 2003). In contrast, Jutila (2001) found a strong and general increase in germination from the soil seed banks in Baltic coastal grasslands when 7 weeks of inundation were followed by a period of draw-down. Comparable phenomena were observed by Schneider and Sharitz (1986) in draw-down parts of a riverine swamp forest after spring floods. Such conditions are quite similar to those prevailing in flood-meadows, whose soil seed bank proved to be rich in species and individuals (Hölzel and Otte 2001). Thus, we suspected that temporary flooding may act as a germination cue (Leck 1989) that enhances recruitment from the persistent soil seed bank. To assess the effects of inter-annual variations in flooding we compared the composition of aboveground vegetation and soil seed banks at field study plots in two years with extremely contrasting flooding conditions. Field studies of year-to-year variation in wetland seed banks are still extremely scarce. The few analyses that were conducted to date, e.g., by Bonis et al. (1995); Leck and Simpson (1995), revealed a predominant impact of contrasting hydrological conditions between years on short term variation in the soil seed banks. The same was expected for the flood-meadows in the present study, although due to our observational approach other agents besides flooding cannot be completely ruled out.

The main questions addressed in this article are:
- how did soil seed banks change in size and composition between the two periods with contrasting flooding conditions,
- did the relationship between soil seed bank and established aboveground vegetation change,
- are there differences in the soil seed bank response among individual species or functional species groups,
- are such different responses related to ecological gradients such as flooding height and diaspore input conditions?

Material and methods

Study sites

The studied flood-meadows are situated in the Holocene floodplain of the northern Upper Rhine, Germany, between the tributaries Neckar to the south and Main to the north (core area: 49°51' N / 8°23' E, 83-91 m a.s.l.). The irregularity of floods in conjunction with the rather dry and warm climate in the region results in a high seasonal and inter-annual variability in soil water potential. Three hydrological compartments can be distinguished within the Holocene flood-plain: The *functional floodplain* is still subject to direct and unhampered flooding during

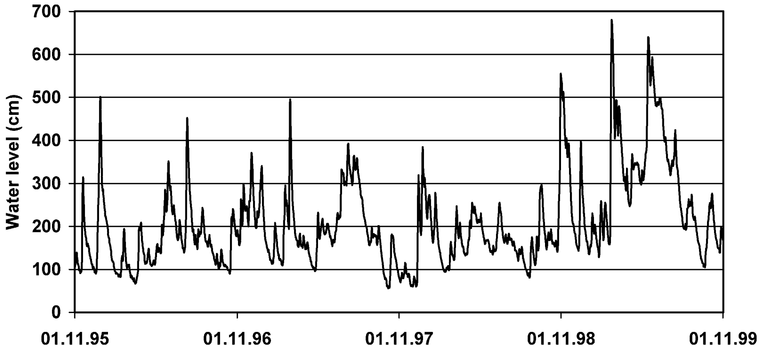

Figure 1. Water levels of the River Rhine at the gauge station of Worms in the two hydrological years before seed bank sampling in September 1997 and 1999. Corresponding grassland communities: 3 to 4 m = *Magnocaricion*; 4 to 5 m = *Cnidion*; > 5 m *Arrhenatherion.*

high water levels of the River Rhine, whereas the *hybrid floodplain* is directly inundated only during extremely high floods that spill over low summer dykes. The *fossil floodplain*, protected by high winter dykes, is only subject to indirect flooding by ascending groundwater (for further details see Hölzel and Otte 2001).

In the functional and hybrid compartments, flooding heights reach a maximum of 3 to 4 meters over terrain and may lead to an almost complete die-back of above-ground biomass in the meadows when floods occur in summer during the main vegetation period (e.g., Vervuren et al. 2003). In contrast, flooding by ascending groundwater in the fossil compartment reaches a maximum height of barely more than 50 cm, which is tolerated by many flood-resistant plants and leads only partly to a die-back in above-ground vegetation. Out of the 46 analysed flood-meadows 18 are situated in the functional, 12 in the hybrid and 16 in the fossil floodplain compartment. Grassland types in the floodplain are typically ordered along an elevational gradient that reflects zones of different average flooding frequency (Dister 1980; Burkart 1998; Hölzel 1999; Leyer 2002). The highest parts of the floodplain that are on average flooded for less than 8 days per year are occupied by mesophytic alluvial meadows (alliance *Arrhenatherion*). At intermediate elevations that are submerged on average for 8 to 26 days per year these are replaced by alluvial wet meadows (alliance *Cnidion*). Grasslands at the lowest elevations, with an average flooding of 26 to 81 days, comprise damp tall sedge meadows (*Magnocaricion*). The majority of sampled stands are situated at the intermediate flooding level of *Cnidion*-communities (34), while *Magnocaricion* and *Arrhenatherion* types are only represented with six stands, respectively. Within these hydrological main types two further important categories may be distinguished that differ considerably from the others in terms of use history and trophic conditions: 8 plots originate from former arable land that was restored into grassland some 15 years ago, whereas 6 plots in the fossil floodplain comprise strictly oligotrophic *Molinion* communities that are confined to particularly nutrient poor sites where the loamy topsoil was removed in the past. The plots in the functional and hybrid compartments are mown once a year in June or July, while in the fossil floodplain compartment mowing usually takes place in September. During the relevant period of observation there were no significant changes in the type and intensity of management in the studied meadows.

Flooding conditions before seed bank sampling

In the two hydrological years before the first sampling in September 1997 only three minor flooding events with water levels above four meters at the nearby gauge of Worms (average mean water level 2.2 m) occurred (Figure 1), none of them lasting for more than three or four days. Compared with the long-term mean this was an unusually dry period (Table 1). Due to low height and short duration of flooding the hybrid and fossil compartments were not inundated at all and even in the functional compartment, the total number of days with water levels above 4 and 5 m reached only 17 and 6%, respectively, compared with the long term average (Table 1). This situation changed completely in the season before the second sampling took place in September 1999. Whereas the hydrological year 1998 was also extremely dry, in 1999 a series of three very high and long lasting

Table 1. Duration of high water levels (in days) of the River Rhine at the gauge station of Worms: A: two hydrological years (01.11.95-30.10.97) before the first sampling; B: two hydrological years (01.11.97-30.10.99) before the second sampling; C: 20 year mean (1981-2000) for two hydrological years. Corresponding grassland communities: 3 to 4 m = Magnocaricion; 4 to 5 m = Cnidion; > 5 m Arrhenatherion. In column A and B two Figures are given: days above water level in the first column / percentage of C.

	Time period		
Gauge height	A	B	C
> 3 m	73 / 45	177 / 108	164
> 4 m	9 / 17	81 / 156	52
> 5 m	1 / 6	31 / 194	16
> 6 m	0	8 / 267	3

floods occurred (Figure 1) in early November (2 weeks), late February/early March (3 weeks) and May/June (6 weeks). The latter was an exceptionally long-lasting early summer flood that was topped during the past 20 years only by a summer flood in 1987, which lasted almost nine weeks. Compared with the two years before the first sampling the duration of flooding at the gauge level above 4 and 5 m increased by a factor of nine and 30, respectively (Table 1). Deviation in flooding duration from the long-term average increased considerably with flooding height and reached almost double values at the level above 5 m. This means that the hydrological conditions at the higher levels of the floodplain differed more strongly from average than in the lower ones.

Sampling

Aboveground vascular plant species composition was sampled each year from 1998 to 2000 on 46 permanent plots (200 m^2) containing two subplots of 100 m^2. Species abundance was visually estimated on a modified Braun-Blanquet-scale (van der Maarel 1979). Sampling of vegetation usually took place in June. In 1999, when the vegetation in most of the plots in the functional and fossil compartments was destroyed by heavy flooding in May/June, sampling was conducted in August after resprouting of the meadows.

Sampling of seed banks was carried out in September 1997 and 1999 using a 3 cm diameter soil corer. Within each 200 m^2 plot 20 cores of 10 cm depth were taken at random locations after thoroughly removing living and dead plant material from the soil surface. The soil cores were then divided into 0 − 5 cm and 5 − 10 cm sections.

We analysed seed banks by the seedling emergence method (Roberts 1981). After removing vegetative plant material, the soil samples were transferred in a 2-3 cm thick layer to 18 x 28 cm styrofoam basins and exposed for 36 months in free air conditions. Germinated seedlings were identified and removed once every few weeks (for further details see Hölzel and Otte 2001). Nomenclature of vascular plant species follows Wisskirchen and Haeupler (1998).

Data analysis

We used the non-parametric Wilcoxon signed rank test for paired samples to test for significant differences between years in seed bank characteristics such as number of seedlings and species, as well as in the proportion of different functional groups. Functional groups such as annuals, perennial ruderals, grasses, meadow forbs and legumes were formed according to data given by Ellenberg et al. (1992) and Grime et al. (1988). A single species could be attributed to one or more groups, e.g., *Trifolium dubium* was included in annuals as well as in legumes. According to the Ellenberg moisture value species were categorised as mesophytes (moisture value ≤ 6) or wetland species (moisture value > 6).

To explore shifts in seed bank community structure we used the DCA ordination, a method of indirect gradient analysis (Jongman et al. 1995). DCA assumes a unimodal distribution of species along gradients. Running a DCA with detrending by 26 segments revealed a gradient length of 5.23 SD units and thus the appropriateness of the DCA. The DCA ordination was performed on square root transformed data matrices to reduce the unduly influence of high seedling numbers on ordination results (van der Maarel 1979). For the same reason, species with less than two occurrences were omitted from the dataset. The DCA ordination graphs were used for a visual determination of main seed bank community types.

We chose the Mantel test to compare the community structure in seed bank and above-ground vegetation matrices before and after disturbance by floods in 1999. The Mantel test evaluates a null hypothesis of no relationship between two distance matrices without any reduction of the underlying species space (Legendre and Legendre 1998). The measure of strength of relationship is expressed by the standardized Mantel statistic (r) that ranges from 1 (high) to

Table 2. Comparison of seed bank properties of 46 samples from flood-meadows in 1997 and 1999. Significant decline (-) or increase (+) according to the non-parametric Wilcoxon test for paired sample: $- = p < 0.001$, n.s. = not significant.

	Year		Change	Wilcoxon
	97	99	%	test
Nº seeds 0 − 5 cm (total)	5282	2687	− 49	−
Nº seeds 5 − 10 cm (total)	2036	1050	− 48	−
Nº seeds 0 − 10 cm (total)	7749	3834	− 51	−
Nº of species 0 − 5 cm	16.3	11.6	− 29	−
Nº of species 5 − 10 cm	10	7	− 30	−
Nº of species 0 − 10 cm	18.7	13.5	− 28	−
Nº of annuals	68.8	32.1	− 53	−
Nº of perennial ruderals	45.7	19.5	− 57	−
Nº of grasses	21.7	12	− 45	−
Nº of perennial meadow herbs	41.3	23.5	− 43	−
Nº of legumes	6.5	4.2	− 35	n.s.
Nº of wetland species	94.5	48.3	− 51	−
Nº of mesophytes	25.8	12.9	− 50	−

− 1 (low). The significance of the correlation was tested using Monte Carlo statistics with 1000 randomised runs (McCune and Mefford 1999). The Mantel test was performed on presence absence matrices using the Sørensen (Bray-Curtis) distance measure.

To describe the changes in the seed bank between the two years of observation, we calculated for each sample pair the Sørensen (Bray-Curtis) distance measure and the % change in total number of seeds and species-richness as well as the % change of certain functional species groups.

For the comparison of these properties by categories such as floodplain compartment and seed bank community type we used the non-parametric Kruskal-Wallis Anova. To evaluate the relationship between the above-mentioned measures of change in the seed bank and flooding duration, we used the non-parametric Spearman rank correlation coefficient. Flooding duration for each plot was calculated from gauge data, field observations and topography.

For DCA ordination and the Mantel test we used the software package PC-ORD 4.0 (McCune and Mefford 1999). All other statistics were performed with STATISTICA 6.0.

Results

A total of 11583 seedlings of 174 species emerged from the seed bank samples. 117 species were recorded in both years, whereas 42 and 15 species were found only in 1997 and 1999, respectively. There was a 50% decline in total number of seedlings between 1997 and 1999 irrespective of the sampling depth (Table 2). The mean number of species decreased by about 30% at both sampling depths. With the exception of legumes, a significant decline could be observed across all functional groups. The decline in annuals and perennial ruderals was about 10% higher than in perennial grasses and meadow herbs. Seed numbers in typical wetland species declined in the same order of magnitude as those in mesophytes.

Response of individual species and species groups

As many as 21 individual species displayed a significant decrease between 1997 and 1999, while only 2 species increased (Table 3). There was also a considerable decline in many other species. These changes were, however, not statistically significant, often due to low frequencies within the dataset. Besides some annual arable weeds, such as *Chenopodium polyspermum, Sonchus asper* and *Capsella bursa-pastoris,* the majority of significantly declining species comprised carpet-forming perennial ruderals such as *Potentilla reptans, Ranunculus repens, Poa trivialis, Taraxacum officinalis, Veronica serpyllifolia* and *Glechoma hederacea*, as well as some ruderal tall herbs such as *Lythrum salicaria* and *Cirsium arvense*. Mesophilious grassland species that are usually confined to the drier parts of flood-meadows, such as *Achillea millefolium*, *Rumex acetosa, Galium verum, Daucus carota, Plantago lanceolata* and *Centaurea jacea* also displayed a significant decline. In contrast, there was no signifi-

Table 3. Comparison of species occurrence in the seed bank of 46 plots in flood-meadows in 1997 and 1999. M = Ellenberg moisture value (1 = very dry to 9 = damp); LF = life form: T = Therophyte, G = Geophyte, H = Hemicryptophyte, Ch = Chamaephyte; LH = life histoy: P = Perennial, A = Annual (w = winter, s = summer), M = Moncarp; CSR = Established strategy (all data derived from Ellenberg et al. 1992 and Grime et al. 1988). Significant decline (-) or increase (+) according to non-parametric Wilcoxon test for paired sample: $-/+ = p < 0.05$, $-/++ = p < 0.01$, $-/+++ = p < 0.001$. Rare species, with less than three occurrences in one year not shown.

					Frequency		Total number		Change		Wilcoxon
Species	M	LF	LH	C-S-R	97	99	97	99	n	%	test
Potentilla reptans	6	H	P	CR/CSR	27	20	392	133	− 259	− 66	−
Ranunculus repens	7	H	P	CR	25	16	310	77	− 233	− 75	−
Cerastium holosteoides	5	Ch/T	P/A	R/CSR	24	15	88	21	− 67	− 76	−
Poa trivialis	7	H	P	CR/CSR	22	25	363	140	− 223	− 61	−
Chenopodium polyspermum	6	T	As	–	22	7	675	217	− 458	− 68	−
Veronica serpyllifolia	6	H	P	R/CSR	21	17	180	115	− 65	− 36	−
Taraxacum officinale agg.	5	H	P	R/CSR	21	8	72	15	− 57	− 79	−
Silene flos-cuculi	7	H	P	CSR	18	16	286	248	− 38	− 13	n.s.
Lythrum salicaria	8	H	P	CR/CSR	18	15	184	50	− 134	− 73	−
Glechoma hederacea	6	H	P	CSR	18	13	63	18	− 45	− 71	−
Achillea millefolium	4	H/Ch	P	CR/CSR	18	9	96	26	− 70	− 73	−
Leucanthemum vulgare	4	H	P	CR/CSR	16	13	51	34	− 17	− 33	n.s.
Poa angustifolia	4	H	P	CSR	15	28	52	135	83	160	++
Veronica arvensis	4	T	Aw	SR	14	14	52	71	19	37	n.s.
Plantago intermedia	7	H	P	R/CSR	14	13	66	72	6	9	n.s.
Rumes acetosa	X	H	P	CSR	14	6	35	10	− 25	− 71	−
Cirsium arvense	X	G	P	C	14	3	25	4	− 21	− 84	−
Sonchus asper	6	T	Aws	R/CR	14	2	25	2	− 23	− 92	−
Arenaria serpyllifolia	4	T	Aws	SR	13	8	33	36	3	9	n.s.
Chenopodium album	4	T	As	R/CR	12	13	114	68	− 46	− 40	n.s.
Juncus articulatus	9	H	P	CSR	12	8	93	45	− 48	− 52	−
Capsella bursa-pastoris	5	T	Asw	R	12	6	71	25	− 46	− 65	−
Lysimachia vulgaris	8	H	P	C/SC	11	14	114	61	− 53	− 46	n.s.
Agrostis stolonifera agg.	X	H	P	CR	10	15	112	49	− 63	− 56	n.s.
Vicia angustifolia		T	Aw	R/CSR	10	13	19	31	12	63	n.s.
Rumex crispus	7	H	P	R/CR	10	6	11	11	0	0	n.s.
Galium verum agg.	4	H	P	SC/CSR	10	3	38	6	− 32	− 84	–
Arabis nemorensis	7	H	P	S/SR	9	9	369	290	− 79	− 21	n.s.
Carex spicata	4	H	P	–	9	5	25	16	− 9	− 36	n.s.
Plantago lanceolata	X	H	P	CSR	9	5	20	6	− 14	− 70	–
Daucus carota	4	H	M	SR/CSR	9	4	25	4	− 21	− 84	–
Carex panicea	8	H	P	S	8	6	89	34	− 55	− 62	n.s.
Pseudolysimachion longifol.	8	H	P	–	8	6	227	75	− 152	− 67	n.s.
Centaurea jacea	5	H	P	S/CSR	8	5	28	10	− 18	− 64	–
Viola pumila	7	H	P	–	7	8	24	22	− 2	− 8	n.s.
Allium angulosum	8	H	P	–	7	6	37	31	− 6	− 16	n.s.
Trifolium repens	5	Ch/H	P	CR/CSR	7	4	13	10	− 3	− 23	n.s.
Urtica dioica	6	H	P	C	7	1	17	1	− 16	− 94	–
Ajuga reptans	6	H	P	CSR	6	7	141	118	− 23	− 16	n.s.
Centaurium pulchellum	X	T	As	SR	6	6	59	14	− 45	− 76	n.s.
Linum catharticum	X	T	B/A	SR	6	6	12	26	14	117	n.s.
Medicago lupulina	4	T	A/P	R/SR	6	4	6	5	− 1	− 17	n.s.
Stellaria media	X	T	Aws	R	6	3	11	3	− 8	− 73	n.s.
Veronica peregrina	8	T	Aws	R	5	7	553	500	− 53	− 10	n.s.
Thalictrum flavum	8	H	P	–	5	5	44	28	− 16	− 36	n.s.
Hypericum perforatum	4	H	P	CR/CSR	5	4	10	10	0	0	n.s.
Juncus alpinus	9	H	P	–	5	4	70	20	− 50	− 71	n.s.
Myosotis arvensis	5	T	Aw	R/SR	5	4	28	12	− 16	− 57	n.s.
Ranunculus polyanthemos agg.	4	H	P	–	5	4	16	7	− 9	− 56	n.s.
Rorippa sylvestris	8	G/H	P	–	5	4	65	59	− 6	− 9	n.s.
Galium album	5	H	P	–	5	3	5	5	0	0	n.s.
Epilobium tetragonum	8	T	Aws	–	5	2	7	2	− 5	− 71	n.s.

Table 3. Continued.

					Frequency		Total number		Change		Wilcoxon
Species	M	LF	LH	C-S-R	97	99	97	99	n	%	test
Carex gracilis	9	H	P	–	5	1	14	1	− 13	− 93	–
Carex tomentosa	7	H	P	–	4	6	10	14	4	40	n.s.
Valerianella locusta	5	T	Aw	SR	4	5	15	15	0	0	n.s.
Allium scorodoprasum	7	H	P	–	4	4	58	12	− 46	− 79	n.s.
Cerastium dubium	7	T	Aw	–	4	4	894	222	− 672	− 75	n.s.
Trifolium hybridum	6	H	P	CSR	4	4	238	123	− 115	− 48	n.s.
Veronica catenata	9	T	A	–	4	4	21	10	− 11	− 52	n.s.
Viola persicifolia	8	H	P	–	4	4	25	6	− 19	− 76	n.s.
Euphorbia esula	4	H	P	–	4	3	18	19	1	6	n.s.
Galium palustre agg.	9	H	P	CR/CSR	4	3	34	6	− 28	− 82	n.s.
Phalaris arundinacea	9	H	P	C	4	3	5	4	− 1	− 20	n.s.
Carex disticha	9	H	P	–	4	2	15	3	− 12	− 80	n.s.
Lotus corniculatus	4	H	P	S/CSR	4	2	10	4	− 6	− 60	n.s.
Poa palustris	9	H	P	–	4	2	12	2	− 10	− 83	n.s.
Persicaria maculata	5	T	As	R	4	2	16	3	− 13	− 81	n.s.
Stachys palustris	7	G	P	CR	4	2	8	2	− 6	− 75	n.s.
Trifolium pratense	X	H	P	CSR	4	1	5	1	− 4	− 80	n.s.
Viola hirta	3	H	P	S	4	1	7	2	− 5	− 71	n.s.
Symphytum officinale agg.	8	H/G	P	C/CR	4	0	6	0	− 6	− 100	n.s.
Lathyrus pratensis	6	H	P	CSR	3	5	5	10	5	100	n.s.
Trifolium dubium	5	T	Aws	R/SR	3	5	7	12	5	71	n.s.
Carex hirta	6	H	P	C/CSR	3	4	57	43	− 14	− 25	n.s.
Anagallis arvensis	5	T	Asw	R/SR	3	3	49	17	− 32	− 65	n.s.
Cardamine parviflora	7	T	Asw	–	3	3	45	48	3	7	n.s.
Carex praecox	3	H	P	–	3	3	6	6	0	0	n.s.
Sagina procumbens	5	H/T	P/A	R/CSR	3	3	4	3	− 1	− 25	n.s.
Chenopodium hybridum	5	T	As	–	3	2	47	10	− 37	− 79	n.s.
Genista tinctoria	6	Ch	P	–	3	2	8	4	− 4	− 50	n.s.
Mentha arvensis	8	G/H	P	C/R	3	2	4	3	− 1	− 25	n.s.
Solanum nigrum	5	T	As	–	3	2	35	2	− 33	− 94	n.s.
Deschampsia cespitosa	7	H	P	SC/CSR	2	7	3	12	9	300	n.s
Prunella vulgaris	5	H	P	CSR	2	7	2	9	7	350	+
Trifolium campestre	4	T	Aw	SR	2	4	9	26	17	189	n.s

cant or only minor decline in many herbaceous species typical of flood-meadows and other wet grasslands such as *Silene flos-cuculi, Lysimachia vulgaris, Rumex crispus, Arabis nemorensis, Pseudolysimachion longifolium, Allium angulosum* and *Viola pumila*. Contrary to the general trend in therophytes, typical winter annuals such as *Veronica arvensis, Arenaria serpyllifolia*, *Vicia angustifolia and Trifolium dubium* did not show any decrease.

Shifts in species composition

The considerable quantitative and qualitative changes in seed bank composition between the two years of observation were also indicated in the DCA graph as a shift of samples in ordination space (Figure 2, Figure 3). By the combination of different ordination axes, five main seed bank community types could be distinguished that reflect analogous differences in aboveground vegetation and site history. Within and among these seed bank community types shifts were rather erratic and equivocal and there was no clear general trend.

Similarity of aboveground vegetation and seed bank

According to the results of the Mantel test (Table 4) the positive relationship in similarity structure between soil seed bank and aboveground vegetation in the following season decreased considerably after major flooding in 1999. The correlation in similarity structure of seed banks before and after flooding was much lower than those in aboveground vegetation, indicating that species composition of seed banks was

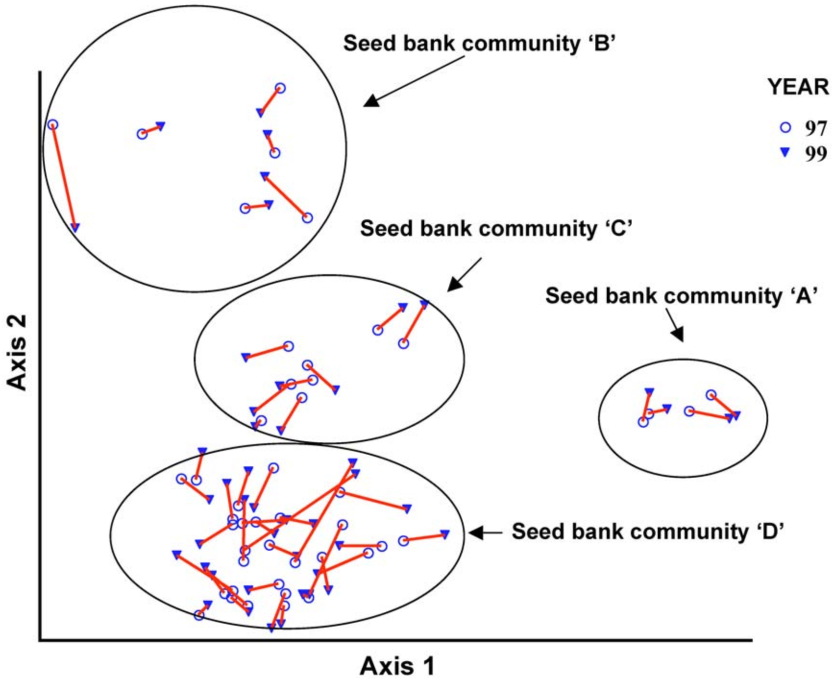

Figure 2. DCA-ordination (Axis 1 and 2) of soil seed bank samples from 46 flood-meadows; vectors connect samples from the same plot in two different years (1997 and 1999). Distinct soil seed bank community types that mostly reflect differences in above-ground vegetation are indicated by numbers: A = *Magnocaricion* meadows, B = *Molinion* meadows, C = *Cnidion* meadows (late mowing), D = *Cnidion* + *Arrhenatherion* meadows (early mowing).

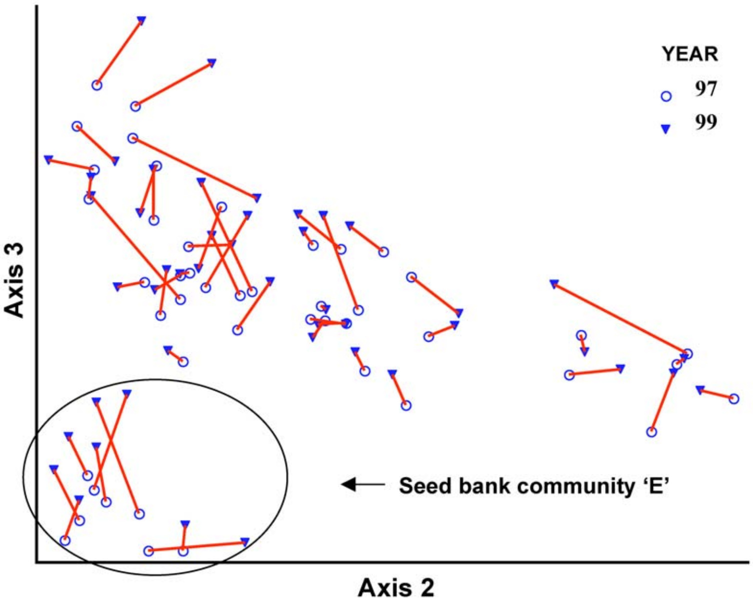

Figure 3. Like Figure 2, but Axis 2 and 3. Seed bank community types: 'E' = former arable fields (out of group D in Figure 2).

Table 4. Evaluation of relationships of seed bank (SB) and aboveground vegetation (AV) distance matrices (n = 41) from different years by Mantel test. r = Standardized Mantel statistics; p = significance of correlation tested by Monte Carlo permutation test with 1000 random runs.

Compared matrices	r	p
SB 97 / AV 98	0.781	0.0010
SB 99 / AV 00	0.621	0.0010
SB 97 / SB 99	0.644	0.0010
AV 98 / AV 00	0.858	0.0010

more strongly affected by flooding than aboveground vegetation.

Seed bank response in relation to environmental gradients and categories

A comparison of traits indicating changes in seed bank properties such as Sørensen similarity measure, the % decline in seed density, species-richness and certain functional species groups by floodplain compartment and major seed bank community types revealed no statistically significant differences among categories (results not shown). Equally, there were no or only minor overall correlations between flooding duration before the second sampling and the % decline of species-richness and seed density in the seed bank (Table 4). Among the functional groups, only grasses showed a significantly higher overall decline with increasing flooding duration, which was also true for the functional and the fossil floodplain compartment. In the hybrid floodplain, the % change in species number in the seed bank was positively correlated with flood duration, which means that there was a higher decline in species at the dryer plots in this compartment. Only in the fossil floodplain compartment did ruderals show a higher % decline with increasing flooding duration.

Discussion

Seed bank depletion by flooding?

The major finding of our study was a heavy and highly significant decline of total seed density and species-richness in the seed banks of the studied flood-meadows within a period of only two years, which took place almost uniformly over different functional groups, vegetation types and hydrological floodplain compartments. Legumes (Fabaceae) were the only functional group that was not significantly affected by the general decline. This is obviously a result of physical dormancy due to a water-impermeable, hard-shelled testa in seeds of this family, which almost generally require scarification to trigger germination (Grime et al. 1981).

The observed short-term seed bank depletion is most probably an effect of the environmental variable flooding intensity, which differed most significantly between both sampling occasions. However, due to our observational approach, other factors besides flooding cannot be completely ruled out, which requires a cautious interpretation of the results obtained.

Firstly, the observed phenomena could be a sampling effect due to small-scaled spatial variability in seed densities within our study plots, or to differences in the timing and method of sampling and seed bank analysis. The latter is very unlikely, since we used absolutely identical sampling times and methods and the determination of seedlings was carried out by the same person and with the same intensity. Equally, small-scaled heterogeneity in seed densities is unlikely to result in a general and highly significant trend of decline over all samples.

Another important factor that has to be considered are inter-annual differences in seed production by the established vegetation, due to changing management or weather conditions that may potentially strongly influence seed bank size and composition (e.g., Thompson and Grime 1979). However, due to the removal of superficial diaspore litter during sampling the effects of short-term seasonal differences in seed production were largely reduced. This is evident from the very low representation of dominant species with high seed production but short-lived seeds during both sampling occasions. Inter-annual differences in seed production will at first influence the upper soil layer, whereas lower soil layers are usually not significantly affected (e.g., Poschlod and Jackel 1993) due to the fact that the burial of seeds is a time-consuming process (Thompson et al. 1997). In our study, however, we found an almost identical decline in total seed density and species-richness, irrespective of the sampling depth, which is hard to explain by inter-annual differences in seed rain. These findings are further supported by the comparison of different floodplain compartments. Whereas the first growth in the functional and hybrid floodplain compartments was completely destroyed by high and long-lasting

Table 5. Spearman rank correlation between flooding duration in the hydrological year 1999 (F) and% change in species number, number of all seeds and of different functional groups in the seed bank of 46 flood-meadow plots. Number of samples per floodplain compartment are indicated in brackets. Significant correlations are given in bold: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

		Floodplain compartment		
	All	Functional (18)	Hybrid (12)	Fossil (16)
F /% species	0.04	− 0.09	**0.62***	− 0.14
F /% all seeds	− 0.16	− 0.06	− 0.07	− 0.46
F /% grasses	**− 0.59*****	**− 0.63****	− 0.34	**− 0.60***
F /% ruderals	− 0.19	− 0.27	0.11	**− 0.57***
F/% annuals	− 0.02	0.02	− 0.00	− 0.06
F /% herbs	− 0.04	− 0.18	0.24	− 0.28

flooding in early summer 1999, the established vegetation of the fossil floodplain was well preserved due to lower absolute flooding height, meaning that in many species seed production could occur largely unhampered. The same was true for the higher levels in the functional and hybrid floodplains, which were flooded only briefly. Given a predominant influence of seed production on the observed depletion of the soil seed bank there should be a divergent response between the different hydrological floodplain compartments and along flooding gradients. However, such patterns could definitely not be found in the analysed seed banks.

A possible explanation for the heavy seed bank depletion we observed could be that the seeds of many species died in the course of long-lasting inundation. Although seeds of certain species, e.g., *Rumex acetosa* (Voesenek and Blom 1992), may be killed by prolonged flooding, seeds generally have a great tolerance towards submergence, even among strictly terrestrial species (Skoglund and Hytteborn 1990; Baskin and Baskin 2001). In our study this was confirmed by the fact that many species which usually avoid moist habitats (Table 3) did not display any decline at all in the seed bank after flooding.

More likely the observed heavy depletion of the soil seed bank may be attributed to a ‘post-flood germination flush’ (Jutila 2001), as has been described in other floodplain habitats (Schneider and Sharitz 1986; Voesnek and Bloom 1992). Floods and the subsequent successive draw-down may facilitate recruitment from the seed bank by prolonged favourable moisture supply and the creation of open gaps due to the complete or at least partial die back of aboveground vegetation (e.g., Leck 1989). Equally, temporary anoxic conditions and increased nitrogen levels may act as a germination cue to break dormancy in certain species (Baskin and Baskin 2001).

Response of individual species in the seed bank

The hypothesis of a post-flood germination flush that led to a temporary depletion in the seed bank of the studied flood-meadows is strongly supported by the patterns of decline and persistence in individual species, in particular with respect to their germination characteristics.

Remarkably, among the most seriously declining species there was a high proportion of nutrient-demanding competitive ruderals such as *Ranunculus repens* and *Poa trivialis.* Typically, plants that follow this strategy exploit turf gaps after disturbances, not only by excessive lateral clonal spread, but also by recruitment from the seed bank (Grime 2001). Among the declining ruderals, there were many species with high germination temperature requirements (> 20 °C), e.g., *Potentilla reptans* (Ziron 2000), *Chenopodium polyspermum* (Otte 1996) and *Lythrum salicaria* (Grime et al. 1981, Patzelt 1998). Flooding in early summer, when such temperature requirements are met, seems to be particularly favourable for these species, since germination from the seed bank in flood-meadows is usually hampered by drought and shading through high and densely developed canopy structures at this time of the year.

Another aspect that must be considered is the input and increased availability of nutrients due to sedimentation as well as intensified mineralisation and decomposition of dead below- and aboveground biomass in the course of flooding events. High nitrate contents proved to be particularly relevant as a cue to trigger germination in darkness in nutrient-demanding annual ruderal species (Bouwmeester and Karssen 1989). Ziron (2000) and Knödler (2001) found a strongly significant increase in germination rates of *Capsella bursa-pastoris* and *Potentilla reptans* in experimental variants with nutrient addition; in *Ranunculus repens* and to a lower degree in *Poa trivialis* germination in darkness was even completely dependent on the addition of nutrients. Comparable results were obtained in *Plantago lanceolata* by Pons (1989), who interpreted the breaking of dark dormancy by elevated nitrate concentrations in the soil as a gap detection mechanism after disturbances in aboveground vegetation.

In contrast to many nutrient demanding ruderals with high temperature requirements, there was no significant decline in typical winter annuals such as *Veronica arvensis*, *Arenaria serpyllifolia, Vicia angustifolia, Trifolium dubium* and *Trifolium campestre.* These species preferably germinate at the beginning of the cool season in autumn, and partly in early spring (Baskin and Baskin 1983a; Grime et al 1988). In *Veronica peregrina,* a typical plant of temporary flooded habitats, Baskin and Baskin (1983b) showed that due to conditional seasonal dormancy the ability to germinate at high temperatures above 20 °C is lost in May and June. In line with this germination behaviour, there was no decline of this species in our study. Comparable conditional dormancy cycles have also been described in perennial species typical of wet meadows, such as *Silene flos-cuculi*, which although abundant in the seed bank did not show any decline after flooding. Exhumed seeds of this species germinated in light all year round but exhibited a cyclic pattern of germination in darkness, with a peak occurring in spring (Milberg 1994). Such dark-dormancy cycles were also found in different *Carex* species of temperate wetlands (Baskin et al. 1996; Schütz 1997).

Summarizing, we can conclude that individual germination characteristics of species, such as temperature requirements, seasonal dormancy cycles and sensitivity to nutrition, gave the best explanation for the patterns of decline and persistence in the soil seed bank after flooding. Significant effects of different temperature regimes in combination with flooding treatments on recruitment from the soil seed bank of temporary wetlands were also described by Seabloom et al. (1998). Judging from the patterns of decline and persistence of certain species in conjunction with their germination requirements and dormancy cycles we suppose that the unusually long lasting early summer flooding had the greatest impact on the observed temporary seed bank depletion, while winter floods, mostly due to low temperatures, should be of lower significance. In seed addition and plant litter transfer experiments in the same year and region, we also observed a strong facilitation in seedling recruitment after early summer flooding in comparison with non-flooded plots (Hölzel and Otte 2003).

Environmental gradients and seed bank depletion

Long lasting early summer flooding is a rather irregular and unpredictable event in the studied flood-meadows, especially at medium and higher elevation, that re-occurs on average one to two times per decade. As indicated by the Mantel test, its effects on the compositional structure of soil seed banks were even more profound than in aboveground vegetation. In aboveground vegetation, such flooding events typically lead to a significant decline in certain flood-intolerant mesophytic species, such as *Arrhenatherum elatius* (Vervuren et al. 2003) and to an increase in abundance and dominance of species that favour damp to wet site conditions (Balátová-Tuláčková 1979, Hölzel unpubl.). In the soil seed bank, both groups may be affected irrespective of their moisture preferences (Table 2). The patterns of decline we observed between sampling plots were hard to relate to environmental gradients and groupings such as flooding duration, flood-plain compartment and seed bank community type. In contrast to other studies that found such relationships and patterns in more or less dynamic wetland ecosystems (van der Valk and Davis 1978; Keddy and Ellis 1985; Gerritsen and Greening 1989; Casanova and Brock 2000; Middleton 2000; Nicol et al. 2003), the analysed flood-meadows are predominantly terrestrial ecosystems in which flooding occurs as a more or less regular but rather short-term and unpredictable disturbance. Aquatic plants that may respond to flooding duration and height are almost completely absent from the studied seed banks. Thus, not flooding itself, but rather the period of successive draw down that provides particularly favourable moisture conditions for germination should be of major significance for the observed seed bank processes (e.g., Nicol et al. 2003). The duration of this period may be influenced by micro-topography, weather conditions and stability of certain water levels but not necessarily by the absolute duration and height of the flooding. This means that favourable germination conditions may occur in a relatively irregular manner, irrespective of elevational gradients. There were also considerable differences in structural features among plots during the relevant period of draw-down in June 1999. These differences, ranging from bare open soil to more or less closed and thick carpets of dead plants, algae (e.g., *Characeae),* and drift material, without or in combination with sparse aboveground vegetation, also occurred in a rather erratic manner. Due their impact on light conditions and soil temperatures they must be seen as another potential source of unpredictable variation, influencing recruitment from the seed bank (e.g., Seabloom et al. 1998). Poor correlations between environmental variables and seedling densities during draw-down were also described by Welling et al. (1988).

Our results clearly suggest that species-specific facilitation of recruitment from the soil bank, as well as persistence in the course of flooding events, have a significant impact on structuring and maintaining the floristic diversity in flood-meadows. In accordance with other studies from dynamic amphibious habitats (e.g., Abernethy and Willby 1999; Brock and Rogers 1998; Bonis et al. 1995), the major ecological function of persistent soil seed banks in flood-meadows appears to be the exploitation and bridging of the effects of highly variable hydrological conditions.

Acknowledgements

For their help with in sampling and taking good care of the emerging seedlings we are grate-full to Lorenz Geissler, Josef Scholz vom Hofe and Kerstin Wahl. Tobias Donath, Lutz Eckstein and Dietmar Simmering provided helpful comments to a former version of this manuscript and Rod Snowdon polished our English. The comments of two anonymous referees greatly improved the quality of this paper. Our work was partly supported by grants from the German Federal Agency for Nature Conservation (BfN).

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