Journal of Vegetation Science 12: 209-218, 2001

The impact of flooding regime on the soil seed bank of flood-meadows

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Abstract. We assessed the significance of flooding for the floristic composition of seed banks in flood-meadows of the northern valley of the Upper Rhine. We compared three hydrological compartments of the alluvial plain, consisting of the regularly flooded land between the river and low summer dykes (functional flood-plain), the occasionally flooded land between summer dykes and high winter dykes (hybrid flood-plain) and the land behind the winter dykes, which is now only submerged by ascending groundwater (fossil flood-plain). Due to their different flooding regime, the three compartments should differ with respect to the prevailing conditions of diaspore input.

The seed density of soil samples increased with the duration of flooding in the three compartments, while species richness and the proportion of species not occurring in the vegetation was constant. The increase in seed density can be largely attributed to an increase of disturbance indicators, which are present in the above-ground vegetation and capable of forming a long-term persistent seed bank.

No effects of flooding on the composition of seed banks in the three flood-plain compartments were found. The differences in seed bank composition can be largely explained by corresponding differences in above-ground vegetation and former and present-day meadow management. Seeds of species absent from above-ground vegetation can be attributed to the local species pool present in the immediate vicinity of the study plots. We discuss consequences of the results for the restoration of species-rich flood-plain meadows.

Keywords: Flood-plain; Restoration; Rhine; Seed dispersal.

Nomenclature: Wisskirchen & Haeupler (1998).

Introduction

In large river valleys influenced by subcontinental climatic conditions the meadows subjected to regular flooding contain a large number of highly specialized, characteristic plant species (alliance *Cnidion sensu* Balátová-Tulaćkova 1969). Due to changes in hydrology and management they have become extremely rare and are considered endangered plant communities (Korneck et al. 1996). Larger Central European remnants of these flood-meadows are found in the catchments of the rivers Elbe and Oder (Burkart 1998; Korsch 1999) and in the plains along the northern Upper Rhine (Dister 1980; Böger 1991; Hölzel 1999). Restoration of flood-plains aiming at the re-establishment of species-rich meadows has been pursued for some 20 years. The reconnection of dyked areas to the flooding regime of the river Rhine is thought to be a prerequiste for the fast restoration of species-rich meadows, partly because diaspores are expected to be transported and deposited in the course of flooding events (Dister et al. 1992).

Flooding is widely regarded as a significant vector of dispersal in flood-plain ecosystems (Sauer 1988; Malanson 1993; Bonn & Poschlod 1998). However, to date there have been few empirical studies on this subject. Almost all previous work was carried out in flood-plain forests (Schneider & Sharitz 1988; Schwabe 1991; Hughes & Cass 1997) or grasslands (Skoglund 1990; Finlayson et al. 1990; Nilsson et al. 1991) in relatively natural flood-plains. In contrast, the anthropogeneous flood-meadows along large rivers with strongly altered hydrological regimes have only rarely been the object of such investigation (McDonald 1993; McDonald et al. 1996; Kleinschmidt & Rosenthal 1995). The sparsity and divergence of findings severely hampers the assessment of the role, which alluvial diaspore transport plays in flood-plain ecosystems in general and in the restoration of flood-meadows in particular (Bakker et al. 1996; Poschlod 1996).

As direct measurement of the quality and quantity of diaspore deposition is fraught with methodological problems due to the irregular nature of flooding events (cf. Skoglund 1990), we tried to assess its significance by analysing the composition of soil seed banks. We made use of the fact, that the persistent part of the seed bank forms an archive reflecting cumulative effects of previous inputs of diaspores over many years (Baker 1989).

Due to the construction of dykes the Holocene flood-plain of the river Rhine is now separated into three hydrological compartments, which differ with respect to the conditions of diaspore deposition during flooding events.

1. The **functional flood-plain** consisting of the land between the river and summer dykes is directly flooded by water loaded with fine sediment during high water of the Rhine. This relatively natural flooding regime theoretically allows a regular and free input of diaspores.

2. The **hybrid flood-plain** which is between summer and winter dykes is only reached by extreme high water, that spills over the summer dykes (from 4 m above mean water level at the water-gauge at Worms upward) or in the event of breaking dykes. At high river levels that do not overtop the summer dykes ground depressions in this compartment may be submersed by ascending groundwater. An input of diaspores from river water may occur at a frequency of ca. three years according to the long-term mean for the period 1977-1996.

3. The **fossil flood-plain** on the landward side of the winter dykes is only submerged in low depressions by the ascent of clear, sediment-free groundwater accompanying high water levels of the Rhine. Deposition of diaspores by river water is precluded.

In this study we compare the seed banks of the three hydrological compartments of the holocene flood-plain and tested the hypothesis that there would be a larger allochthonous influence on the soil seed bank in the functional flood-plain and a smaller influence in the hybrid flood-plain. This hypothesis implies that seed banks in the functional flood-plain should have larger numbers of seeds and a significantly higher proportion of species absent from the existing above-ground vegetation, which are supposed to be induced during floods from the upstream part of the catchment (Hughes & Cass 1997). These effects are expected to be most marked at the lowest levels of the functional flood-plain, which are subject to most frequent flooding. We therefore first investigated gradients of flooding frequency within the three flood-plain compartments.

The questions addressed in this paper are:

1. Can significant quantitative and qualitative differences in the seed bank of flood-meadows be measured along a gradient of flooding frequency?
2. Are different flooding regimes in the hydrological compartments of the Rhine flood-plain reflected in the respective seed banks?
3. Do properties of the seed banks support the assumption that diaspore input via flooding contributes to the restoration of species-rich flood-meadows?

Methods

Study sites

The sampling plots are situated in the Hessian portion of the Holocene flood-plain along the northern Upper Rhine between the tributaries Neckar to the south and Main to the north. The meadows of the studied type occupy fine-grained calcareous alluvial soils, which are irregularly flooded during high water levels of the Rhine. In conjunction with the warm and rather dry climate of the region (10.3 °C mean annual temperature and 580 mm annual precipitation, at the meteorological station of Worms; Müller-Westermeier 1990) this results in high variability of soil water potential. While winter, spring and early summer often bring floods, summers may be markedly dry. These conditions are similar to those prevailing along the large rivers of the eastern European lowlands, which is reflected in the occurrence of specialist plants of subcontinental distribution such as *Allium angulosum*, *Cnidium dubium*, *Scutellaria hastifolia* and *Viola pumila*, which are close to the northwestern limits of their areas (Hultén & Fries 1986).

Flood-meadows are differentiated along an elevational gradient of decreasing flooding frequency (Dister 1980; Hölzel 1999). The highest levels of the flood-plain, which are submerged for less than eight days per year in the long-term mean, are occupied by alluvial *Arrhenatherion* communities. *Allium angulosum-Alopecurus pratensis* flood-meadows (*Cnidion*) occur at intermediate elevation subject to 8-26 days of flooding per year. The lowest level with 26-82 days of flooding per year is covered by *Rumex crispus-Poa palustris* flood-meadows (*Magnocaricion*) typically dominated by reed and swamp species (Dister 1980). In principle this sequence is also valid in the hybrid and fossil compartments of the flood-plain, although their hydrology is complicated by the dynamics of pressure water and flooding frequency, which cannot be estimated directly from the level of the river Rhine (Böger 1991).

Sampling

The sampling of above-ground vegetation and seed banks was carried out on permanent quadrats spread out over the whole study area. 16 plots were situated in the functional, 12 in the hybrid and eight in the fossil flood-plain. The majority of stands (12) in the functional compartment are *Allium angulosum-Alopecurus pratensis* flood-meadows, while lower-elevation reed swamps (*Magnocaricion*) and higher elevation meadows (*Arrhenatherion*) are represented by two plots each. Half of the 12 plots in the hybrid flood-plain are *Cnidion*-meadows, half are alluvial *Arrhenatherion*-meadows; four of the latter originated from arable fields 15 years ago. The plots in the fossil compartment are in low-lying depressions regularly submerged by groundwater and are classified as *Cnidion*-meadows.

The plots in the functional and hybrid compartment are situated within a distance of 500 to 2500 m from the recent main channel of the river Rhine. Most of the plots in the functional compartment are found along ancient, silted up river channels, which are directly connected to the main channel during high water levels.

While meadows in the fossil flood-plain are mown late in the year (August/September) and irregularly, the stands of the hybrid and functional compartments are regularly mown once or twice with a first cut in June. With the exception of two plots in the hybrid flood-plain the plots receive no fertiliser.

Above-ground vegetation

Above-ground vascular species composition was sampled on 200+m^2 permanent plots containing two subplots of 25 m^2 nested within two subplots of 100 m^2. Species abundance was visually estimated on a modified Braun-Blanquet-scale with cover degree 2 subdivided into 2m, 2a and 2b (van der Maarel 1979). Prior to data analysis we pooled the samples of the very dry year 1998 with those of 1999, when flooding was unusually intense, so that we were able to survey species composition in two years with substantially different ecological conditions. Re-sampling in the wet year 1999 added a considerable number of species to the list.

Seed bank

Sampling of seed banks was carried out in September 1997 using a soil corer of three cm in diameter. 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. Thus the data represent the soil seed bank in the strict sense without the superficial diaspore litter deposited in the sampling year (Urbanska 1992). The soil samples represent 141 cm^2 of the soil surface and 1410 cm^3 of the soil volume in each plot and were thus well above the minimum requirements for studies of seeds in grassland given by Oomes & Ham (1983).

We analysed seed banks with the seedling emergence method (Roberts 1981). After removing vegetative plant material the soil samples were transferred in a two to three cm thick layer to 18 cm × 28 cm styrofoam basins and exposed in free air conditions. The basins were protected against diaspore input and heating by covering them with flat, white gauze lids. Control basins filled with sterile soil were placed between the samples. In summer the basins were watered regularly. Germinated seedlings were identified and removed once every few weeks. Unidentifiable specimens were transferred to pots and grown until they could be named. When germination declined, the samples were dried for two weeks in a greenhouse, the soil material was crumbled, mixed, watered and again exposed in free air. The seed bank study was continued for 36 months. After 24 months < 1% seedlings and no additional species were recorded.

Data analysis

We classified the longevity of seeds according to the three categories proposed by Thompson et al. (1997) and by using the extensive database contained in their book:

- transient: persistent for < 1yr;
- short-term persistent: 1-5 yr;
- long-term persistent: > 5 yr.

Regarding established vegetation and soil seed bank at two depths like Thompson et al. (1997), we classified species not mentioned in their database.

As allochthonous we define species in the seed bank, which were never recorded in the above-ground vegetation of the plots during two years of sampling.

For plots in the functional flood-plain we calculated the mean annual duration of flooding for the period 1977-1996 by using data from the gauge of the river Rhine at Worms and topography. Additionally unweighted mean Ellenberg indicator values for moisture were calculated for above-ground vegetation plots on the basis of the list given by Ellenberg et al. (1991). In the functional flood-plain the mean Ellenberg values for moisture showed a high correlation with the directly measured values of mean flooding duration derived from the gauge (Spearman's $r = 0.87$, $P = 0.000052$). Thus we used the mean Ellenberg values to describe the flooding situation in the hybrid and fossil compartment, where the mean annual duration of flooding cannot be derived directly from the Rhine water level.

We correlated environmental variables and properties of the seed bank using non-parametric Spearman's r. For normally distributed data with homogeneous variances/covariances (Sen & Puri test) we compared means using the parametric Tukey Honest-Significance test (HSD) for unequal sample sizes. For non-normal data, first a Kruskal-Wallis-Anova was performed; second pairwise differences between categories were checked by multiple non-parametric Mann-Whitney U-tests using Bonferroni-corrected significance levels.

All calculations were performed on log-transformed species data matrices (cluster analysis, CCA, ANOVA). Species with less than four occurrences and two samples from the functional flood-plain with extreme high values in diaspore densities were eliminated in these analyses. Except for the ordinations all calculations were carried out using STATISTICA 5.1 for Windows 97 (Anon. 1998).

We classified seed banks using the Ward clustering algorithm (Jongman et al. 1995) with the squared Euclidean distance as a measure of dissimilarity. To identify possible factors controlling seed bank composition we used ordinations carried out by CANOCO 4 software (ter Braak & Šmilauer 1998). We first per-

Table 1. Composition of the seed banks in meadows of the functional flood-plain along an elevation gradient (3 m) of increasing duration of flooding. The first five samples are ordered along a transect (horizontal distance 100 m, vertical distance 2 m), the last two samples, representing rare flood-meadows with extremely long flooding duration, are added from an other site. Figures are no. of seeds/sample (141 cm^2 × 10 cm). Seed numbers: in bold = species present in above-ground vegetation and seed bank; underlined = species absent from the above-ground vegetation samples both in 1998 and 1999, but present within less than 100 m around the sampling plots; in italics = species absent from the above-ground vegetation samples both in 1998 and 1999 and not found within 100 m around the sampling plot.

	Arrhenatherion		*Cnidion*			*Magnocaricion*	
IDays of flooding/year	1	6	10	20	25	82	82
Indicator value for moisture	4.5	4.7	4.9	5.4	5.8	7.5	7.5
Total no. of seeds	38	58	105	98	124	756	823
No. of seeds/m^2	2260	4060	7350	6860	8680	52920	57610
No. of species	15	13	19	13	13	17	12
Galium album	**1**						
Viola hirta	**2**						
Vicia angustifolia	**2**						
Linum catharticum	**2**						
Ajuga reptans	**3**						
Ranunculus polyanthemophyllos	**4**						
Arenaria serpyllifolia	*6*						
Trifolium pratense		1					
Carex praecox		**3**					
Achillea millefolium		**1**	**1**				
Allium scorodoprasum		**14**	**32**				
Plantago lanceolata	**1**	2	**3**				
Rumex acetosa/thyrsiflorus	**3**	**4**	**5**				
Poa angustifolia	**7**	**10**	**4**	**1**	**5**		
Veronica arvensis	**3**	**4**	**2**	**9**	**3**		
Taraxacum officinale agg.	**1**	1			**3**		
Cerastium holosteoides		**4**	**1**	**3**	**2**		
Veronica serpyllifolia		10	24	**35**	**17**		
Leucanthemum ircutianum		3		**1**			
Trifolium dubium				**3**			
Galium wirtgenii			**6**	**6**			
Carex spicata			**1**	**2**	**1**		
Glechoma hederacea			**2**		*4*		
Potentilla reptans			**2**	**18**	**12**		
Poa trivialis			4	14	18	**6**	
Ranunculus repens		1	4	**2**	**30**	**52**	**28**
Silene flos-cuculi			1	**3**	**27**	**22**	**19**
Cerastium dubium						**401**	**454**
Veronica peregrina						**190**	**147**
Trifolium hybridum						**41**	**100**
Cardamine parviflora						**16**	**22**
Plantago major intermedia						**8**	**24**
Veronica catenata						**3**	11
Galium palustre						**2**	**11**
Carex acuta						**4**	**3**
Rorippa sylvestris						**3**	
Rorippa amphibia						**3**	
Poa palustris						**2**	
Rumex crispus						**1**	
Lythrum salicaria						1	
Myosotis scorpioides agg.							**1**
Trifolium repens							1
Species not typical of meadows							
Sonchus asper	1						
Chenopodium polyspermum	*1*		*2*				
Cirsium arvense			1				
Urtica dioica			1	1			
Artemisia vulgaris			4				
Lapsana communis					1		
Ranunculus ficaria					1		
Galeopsis tetrahit						1	
Unidentified	1		5				2

formed a Detrended Correspondence Analysis (DCA, with detrending by segments) of the above-ground vegetation species matrix resulting in four ordination axes representing 40.5 % of the total variance in species data. The first axis had a length of 2.235 standard deviation units, which indicates the appropriateness of a unimodal response model. The sample scores of the four DCA-axes were subsequently used as constraining ('environmental') variables in canonical correspondence analyses of the seed bank matrix. We also selected the following additional constraining variables: Mean Ellenberg indicator value for moisture (Ellenberg et al. 1991) and dummy variables for time of mowing (early, late) and previous use as arable field. The different diaspore input conditions of the three flood-plain compartments were described as an ordinal variable in a ranking order from fossil (0), through hybrid (1) to functional (2). In the ordination diagram this ordinal variable was treated like a quantitative variable (Jongman et al. 1995). We did explicitly not use soil chemical variables such as organic matter content, C/N-ratio, CAL-soluble P and K in the topsoil, as these have been previously shown to have little direct influence on seed bank composition (Bekker et al. 1997). To test the choice of unimodal species responses we performed a detrended CCA (detrending by segments), which gave a gradient length of 2.831 for axis 1. In order to isolate the effect of flood-plain compartment on seed banks we performed a decomposition of variance by running a series of partial CCAs as proposed by ter Braak & Šmilauer (1998, p. 258).

Table 2. Relationships between mean duration of flooding (mF) calculated from data of the Worms gauge, mean Ellenberg indicator value for moisture (mM) and seed bank variables (Spearman rank correlation); allocht. = only species absent from above-ground vegetation; otherwise total numbers of species and seeds are given including allochthonous species. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

	Variable pair		Spearman ρ	*P*
Functional flood-plain *n* = 16	mF / *n*	Seeds 0-5	**0.50**	0,0505
	mF / *n*	Seeds 5-10	**0.70**	**
	mF / *n*	Spec. 0-10	– 0.21	n. s.
	mF / *n*	Spec. allocht.	– 0.10	n. s.
	mF / *n*	Seeds allocht.	0.01	n. s.
	mM / *n*	Seeds 0-5	**0.56**	*
	mM / *n*	Seeds 5-10	**0.80**	***
Total flood-plain *n* = 36	mM / *n*	Seeds 0-5	**0.54**	***
	mM / *n*	Seeds 5-10	**0.64**	***
	mM / *n*	Spec. 0-10	0.18	n. s.
	mM / *n*	Spec. allocht.	– 0.13	n. s.
	mM / *n*	Seeds allocht.	– 0.00	n. s.

Results

Influence of flooding on seed banks

Table 1 illustrates the differences in seed bank species along a gradient of increasing flooding in a sample of seven plots in the functional flood-plain. The composition of seed bank changed considerably with increasing flooding duration which was also the case in above-ground vegetation. The total number of seeds increased, while total species richness was not affected. *Rumex crispus-Poa palustris* flood-meadows that would be subject to frequent and very long inundation periods had seed densities of more than 50 000 seeds/m^2, more than 80 % of which were contributed by a few therophyte species such as *Cerastium dubium* and *Veronica peregrina*. Likewise in *Allium angulosum-Alopecurus pratensis* flood-meadows a small number of perennial species like *Veronica serpyllifolia*, *Potentilla reptans* and *Poa trivialis* contributed most of the seeds.

Seed density at soil depth 5-10 cm was significantly positively correlated to the duration of flooding (Table 2), whereas at soil depth 0-5 cm a trend was visible, but not significant. The correlation between mean indicator value for moisture and seed density was also significant, which did not change when the 36 sampling plots from all flood-plain compartments were included. In contrast, there was no significant relationship between seed bank species richness or the number of allochthonous seeds and the duration of flooding or the moisture value.

Comparison of seed banks by hydrological flood-plain compartments

The seed banks in the fossil flood-plain contained significantly more seeds at depth 0-5 cm and had a higher species richness than the functional and hybrid compartments (Table 3). It also had significantly higher total numbers of seeds (0-10 cm) than the functional flood-plain. Other differences were not significant.

The cluster dendrogram (Fig. 1) shows clear differences in seed bank classification for the three flood-plain compartments at a residual sum of squares of 50 %. Only two seed banks situated on particularly low ground in the hybrid flood-plain were classified along with the samples from the functional compartment, while, conversely one *Arrhenatherum* meadow at higher level in the functional compartment was grouped with the hybrid flood-plain samples. The dendrogram indicates a higher degree of similarity between the seed banks of the functional and the hybrid compartments, while the samples from the fossil flood-plain are more remote from the remainder.

In the ordination diagram of the CCA with all con-

Table 3. Mean number and standard error of seed bank variables in the three flood-plain compartments; A = functional flood-plain; *n* = 14 (*16), B = hybrid flood-plain; *n* = 12, C = fossil flood-plain; *n* = 8; different letters indicate significant differences ($P < 0.05$) according to Tukey HSD Post hoc-Test for unequal *n*; *n* Seeds = mean number of all seed, *n* Spec. = mean number of species; allocht. = species absent from above-ground vegetation.

		A	B	C	*P*
n Seeds/m^2	0-5	4795 ± 526^a	5221 ± 991^a	9109 ± 1274^b	**
n Seeds/m^2	5-10	1870 ± 233	3372 ± 725	2957 ± 454	n.s.
n Seeds/m^2	0-10	6665 ± 680^a	8593 ± 1526^{ab}	12066 ± 1520^b	*
n Spec.	0-10*	16.6± 1.1^a	16.3 ± 0.9^a	22.4 ± 1.7^b	*
n Spec. allocht.	0-10*	3.3 ± 0.5	5.7 ± 1.1	4.1 ± 0.4	n.s.
n Seeds allocht./m^2	0-10	1106 ± 196	2744 ± 1267	1477 ± 630	n.s.

straining variables included (Fig. 2) a gradient from functional- and hybrid- to fossil flood-plain samples is visible along the first axis. Two out of four above-ground vegetation DCA-axes loaded strongly on axis 1, as did the indicator value for moisture and late mowing. Axis 2 ordered stands mainly with regard to their position in the functional or in the hybrid flood-plain. One above-ground vegetation DCA-axis and previous use as arable field loaded relatively strongly on axis 2 as well. The constraining variables explained 46.3 % of the total variance in the composition of the seed banks (Table 4).

Taken as the only constraining variable in CCA the flood-plain compartments explained 11.8 % of the total inertia (Table 4). However, if all remaining environmental variables were defined as covariables in partial CCA, explained variance dropped to as little as 3.2 % and was no longer significant. In contrast after adjustment for the compartment membership the other environmental variables together still explained 34.6 % of the variance, with existing above-ground vegetation and management as the most important one.

Table 4. Results of various CCA analyses isolating the effect of floodplain compartment and other environmental variables on the soil seed bank. Expl. var. = Explanatory variables; Covar. = Covariables; Eigenv. = Sum of all canonical eigenvalues – measure for explanatory power of the explanatory variables (total inertia = 2.744); % = percentage of explained variance; F = F-ratio statistics for the test on the trace; *P* = corresponding probability value obtained by the Monte-Carlo-permutation test (199 permutations). Explanatory variables: C = floodplain compartment; V = existing above-ground vegetation, M = recent and former management, F = mean Ellenberg value for moisture.

Expl. var.	Covar.	Eigenv.	%	*F*	*P*
M, F, C, V	-	1.27	46.3	2.70	0.005
C	-	0.32	11.8	4.26	0.005
C	M, F, V	0.09	3.2	1.48	0.055
M, F, V	C	0.95	34.6	2.30	0.005
V	C	0.68	24.7	2.73	0.005
M	C	0.36	13.2	2.63	0.005
F	C	0.22	8.1	3.12	0.005

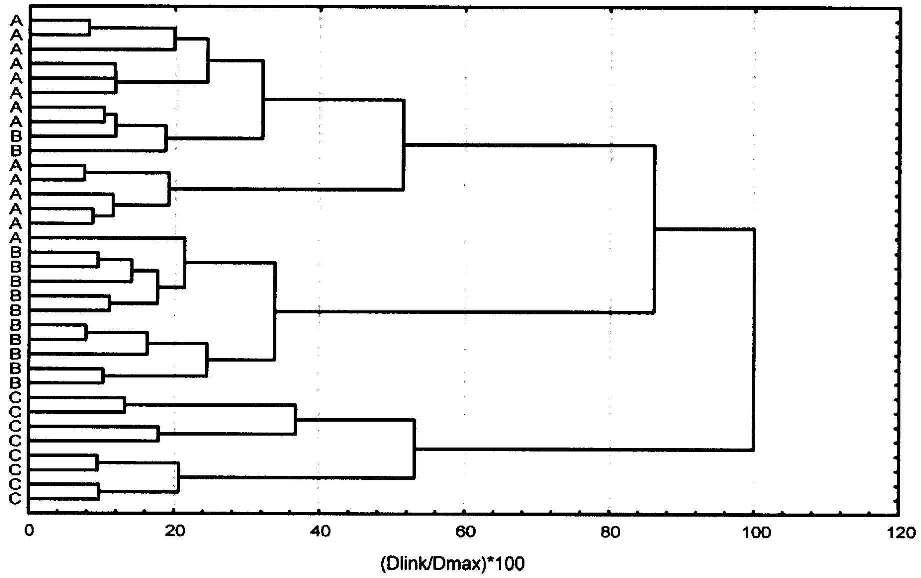

Fig. 1. Cluster dendrogram of 34 seed bank samples from flood-meadows calculated by the Ward algorithm with squared Euclidean distance; A = functional flood-plain, B = hybrid flood-plain, C = fossil flood-plain.

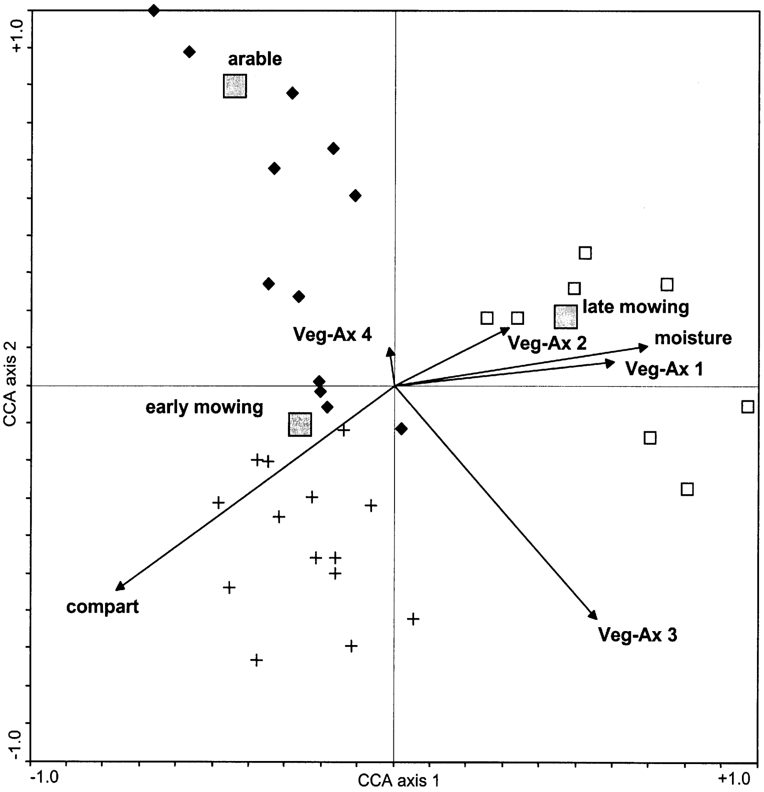

Fig. 2. Canonical Correspondence Analysis diagram in biplot scaling showing the position of seed bank samples in relation to environmental variables. Vegetation axes as explaining variables are derived from a Detrended Correspondence Analysis of above-ground vegetation at the sample sites. Nominal and ordinal environmental variables are given as arrows; categorical variables are given as grey squares by their centroid. Origin of samples: crosses = functional flood-plain; diamonds = hybrid flood-plain, squares = fossil flood-plain.

Comparison of species composition

Of all 140 species found in the soil seed banks 17 exhibited a pattern that depended significantly on flood-plain position (App. 1). The differences were most marked between the functional and the hybrid on the one hand and the fossil flood-plain on the other. Most of the species, which were missing or extremely infrequent in the functional and hybrid compartments, were also absent from the above-ground vegetation of these compartments (*Arabis nemorensis*, *Pseudolysimachion longifolium*). Functional and hybrid flood-plain differed mostly by the occurrence of arable weeds such as *Chenopodium album*, *Capsella bursa-pastoris* and *Stellaria media* in their soil seed banks.

Among the allochthonous species *Veronica serpyllifolia* was characteristic of functional flood-plain seed banks, while *Juncus articulatus* in particular and, less markedly, *Centaurium pulchellum* were preferably found in the fossil compartment. All other statistically significant differences between compartments corresponded to differences in the above-ground vegetation.

Discussion

Influence of flooding duration on the seed banks

Although the studied flood-meadows were subject to marked changes in water availability, which included extended periods of drought, there was a clear increase in seed density in the soil with increasing duration of flooding. The fact that this relationship was particularly strong at a depth of 5-10 cm may be interpreted as a result of the lower susceptibility of this portion of the seed bank to seasonal variations in climate and flooding. The fraction of the lower soil depth thus best represents a mean state of the systems. Increases of seed density with soil moisture have been found in numerous studies of mesotrophic to eutrophic wet meadows (e.g. Chippendale & Milton 1934; Champness & Morris 1948; Thompson & Grime 1979), where the increase in seed density was mainly due to various species of *Juncus*. As shown by Bekker et al. (1998) the survival of seeds of *Juncus* and some other species typical of wet meadows seems to be favoured by anoxic conditions prevailing under constant high groundwater levels.

In flood-meadows with a variable moisture regime as in this study, the genus *Juncus* is hardly represented (cf. McDonald et al. 1996). The increase in seed density was mainly contributed by turf gaps colonising indicators of disturbance such as *Ranunculus repens, Potentilla reptans, Poa trivialis* and *Veronica serpyllifolia*, which increased with flooding frequency also in above-ground stands. At the lowest, frequently flooded levels of the flood-plain the seed bank of flood-meadows was dominated by high densities of seeds of ruderal therophytes such as *Cerastium dubium, Cardamine parviflora* and *Veronica peregrina*, which reflected a higher frequency of disturbance and unstable ecological conditions (Grime et al. 1988).

Higher seed densities associated with frequent flooding in flood-meadows do not seem to be a result of conditions that are more favourable to seed persistence, such as frequent water saturation and poorly aerated soil (Baskin & Baskin 1989; Bekker et al. 1998), but of a change in predominant plant strategy types. This is reflected by the more frequent occurrence of species capable of forming large and long-lived seed banks, which must be considered an adaptation to high interannual variation of ecological conditions (Leck 1989; Poschlod 1996). It is remarkable, that as much as 50% of the specialized large-river macrophyte species (*Viola pumila, Arabis nemorensis, Pseudolysimachion longifolium, Cerastium dubium, Cardamine parviflora* among others) form persistent seed banks. A comparable situation has been reported by Finlayson et al. (1990) from northern Australian flood-plains, by van der Valk (1981) for temporary lakes in North American prairies and by Bekker et al. (1999) for dune slacks on the Dutch North Sea coast.

The seed numbers that we measured in *Cnidion*-flood-meadows of intermediate elevation and flooding frequency are within the range reported by McDonald et al. (1996) from ecologically similar grasslands on the river Thames in southern England. However, they are markedly lower than those under Central European wet meadows in minerotrophic fens and mineral swamps (Fischer 1987; Schopp-Guth 1997), which is mainly due to the low abundance of *Juncus* seeds.

Alluvial influences on the seed bank

The differences in seed bank composition as reflected in cluster analysis (Fig. 1) can, according to CCA results (Fig. 2), be largely explained by analogous gradients in the above-ground vegetation and present use of the study meadows. The study provided no indication for the expected strong allochthonous influences on seed banks in the functional flood-plain. The higher seed density in the fossil flood-plain may be due to the more extensive management with late mowing that this compartment receives, which is likely to enhance the deposition of seeds.

The seed bank species that were not present in the vegetation stands were almost exclusively present in the local species pool of the immediate surroundings of our plots and would probably establish successfully after long periods of inundation. Thus, we observed a sudden development of *Veronica serpyllifolia* and *Chenopodium polyspermum* after major floods in 1999, both species, which had previously been found in the seed bank only. This illustrates, that in flood-plains a single vegetation survey is insufficient for identifying the allochthonous status of species, that may establish large populations from the seed bank only after major disturbances of the turf by flooding instead of being deposited by floodwater. The conjecture, that allochthonous seeds are imported from nearby sources, is supported by the strong occurrence of arable weeds in the hybrid flood-plain. These weeds are not restricted to former fields but appear also in plots, which have never been subject to agricultural use, but are situated in the vicinity of present-day or former arable fields. This finding may be explained by a residual enrichment of seeds derived from adjacent fields in low elevation depressions during the retreat of high waters. In the functional flood-plain, where arable fields are non-existent we never found such high densities of weed seeds.

Other authors have obtained similar results indicating the significance of flooding for short-distance dispersal of seeds (Schneider & Sharitz 1988; Skoglund 1990; Schwabe 1991; Kleinschmidt & Rosenthal 1995). Yet in all these studies there were also seeds attributable to long-distance transport by floods. In contrast to most other studies Hughes & Cass (1997) found very high proportions of allochthonous seeds in river margin forest in Vermont/USA: of 73 species occurring in the soil seed bank and fresh alluvial sediment only 25 were also present in above-ground vegetation. However, these authors did not discuss the possibility of nearby occurrence of some of these species.

In our investigations seeds strongly suggesting remote transport were rare exceptions. One reason for this surprising result could be that most of the above-mentioned studies were carried out in close proximity to riverbeds with more natural morphology and hydrology. Such flood-plains may have substantially more potential seed sources to be dispersed with flooding than is the case along the largely confined Upper Rhine, which has lost most of its natural flood-plains.

A second reason could be the considerable distance of our study plots from the river. Skoglund (1990) and Schwabe (1991), for example, found seeds indicative of long-range transport mainly in drift or sediment deposited close to the riverbank. The flood-meadows in our study, on the other hand, are hardly reached by substantial loads of mineral and organic sediment even by exceptional floods because of their remoteness from the river and the resulting low speed of water movement (Dister 1980). It is in these areas with low sediment loads and relatively low nutrient availability where most present-day and potential sites for species-rich flood-meadows are situated.

Conclusions for restoration management

Our comparative study of seed banks in meadows along the Rhine yielded no indication of significant remote input of seeds in the functional flood-plain. Weedy and ruderal species widespread in the Rhine catchment, such as *Chenopodium album*, *Capsella bursa-pastoris* or *Stellaria media*, were surprisingly entirely absent from seed banks of the functional flood-plain.

Considering the absence of these common species capable of forming persistent seed banks, the probability of much rarer species to arrive by remote transport in floods must be considered as nearly non-existing. If we further consider that the majority of upstream remnants of species-rich flood-meadows containing the target species of conservation is restricted to dyked fossil compartments of the plain (Thomas 1990), long-distance input is largely impossible under the given conditions. However, along with the results of Kleinschmidt & Rosenthal (1995), our study also stresses the significance of inundation for short-distance dispersal of seeds. This possibility requires viable populations of the target species in the vicinity of restoration areas.

In summary we conclude that limited dispersal, which has been identified as one of the main obstacles to restoring rare species in grasslands (Bakker et al. 1996), is unlikely to be overcome by the restoration of more natural flooding regimes under the present-day conditions prevailing along most Central European rivers. As in many other cases, the successful restoration of flood-meadow target species crucially depends on supplementary measures like the transfer of seeds with plant litter from source populations (cf. Patzelt 1998).

Acknowledgements. We would like to thank Lorenz Geissler, Petra Göbel and Ines Klingshirn for their help with taking the soil samples and performing vegetation analyses, and Tobias Donath, Josef Scholz-vom Hofe and Kerstin Wahl for taking good care of the emerging seedlings. Lutz Eckstein, Dietmar Simmering, Rod Snowdon and in particular Jörg Ewald provided helpful reviews and improved our English. We are thankful to J.P. Bakker, J. Lepš and J.R.B. Tallowin, who gave many suggestions for improvement of a former version of this paper.

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Received 22 May 2000;
Revision received 18 October 2000;
Accepted 1 November 2000.
Coordinating Editor: J.P. Bakker.

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