Professur für Landschaftsökologie und Landschaftsplanung
der Justus Liebig-Universität Gießen

Restoration of flood meadows - the importance of seedbanks, dispersal, recruitment and agricultural management

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Dipl.-Ing. agr. Tobias W. Donath

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Dekan: Prof. Dr. Wolfgang Köhler
1. Gutachterin: Prof. Dr. Dr. Annette Otte
2. Gutachterin: Prof. Dr. Angelika Schwabe-Kratochwil

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In paper **I**, I did most of the fieldwork, laboratory work, and had the main responsibility for the data analysis and writing. The co-authors contributed invaluable ideas and suggestions for this study. In case of paper **II,** both first authors contributed equally to the genesis of the paper, i.e. they designed the study, did the fieldwork and had the main responsibility for data analysis as well as writing, while the other co-authors contributed valuable ideas and comments. In the papers **III** and **IV**, I performed most of the realisation, data analysis and writing of the papers. The co-authors were involved in design, fieldwork and result evaluation of these studies.

Table of content

1 General introduction

Intensified management lead to a steep decrease of species-rich grassland communities in Central Europe (Joyce & Wade 1998; Rennwald 2000). But abandonment took its toll, too, especially when only small and isolated remnant stands were left. In addition, wet grasslands were prone to losses through drainage which in many cases eventually resulted in the conversion of these meadows into arable fields. These processes took place in flood-meadows along all large rivers in Central Europe (e.g., Rhine, Elbe, Danube) and left flood meadows of the alliance *Cnidion* behind as one of the most threatened plant community in Germany and Central Europe (Ssymank et al. 1998; Rennwald 2000). Due to these considerable losses the preservation and restoration of alluvial grasslands is presently one of the major topics in several large-scale floodplain research and restoration projects (BMBF 1995; Šeffer & Stanová 1999).

Also along the northern Upper Rhine about 300 ha of former arable land have been converted into grassland, after the opening of dykes, in the early 80s (Dister et al. 1992). The former arable land was either left to self-greening or sown with species-poor seed mixtures of common grasses. But still typical species of flood meadows, such as *Arabis nemorensis*, *Cnidium dubium*, *Iris spuria* and *Viola pumila*, which are not only regarded as threatened in Germany (Korneck et al. 1996) but are even of Central European conservation concern (Schnittler & Günther 1999), are mostly confined to small remnant stands in the study area.

The impact of site conditions and dispersal

The rationale of several large-scale restoration projects has been that after the reduction of nutrient availability through harvest of aboveground biomass target species will readily re-colonize the restoration sites from nearby remnant stands or from viable seeds in the soil seedbank (Bakker & Berendse 1999). However, most of these projects that mainly relied on such passive restoration measures experienced only evanescent success since target species and communities often were not re-established, even when the soil nutrient status and the biomass production were successfully lowered (Graham & Hutchings 1988; Bakker 1989; Berendse et al. 1992). In such cases, limited dispersal was identified as the main obstacle in restoring species-rich grasslands (Bakker et al. 1996; Hutchings & Booth 1996a; Stampfli & Zeiter 1999). Dispersal is most often hampered by spatial isolation, the lack of viable source populations of target species in the vicinity of restoration sites and the absence of traditional dispersal vectors in modern agricultural landscape (Bonn & Poschlod 1998; Muller et al. 1998; Verhagen et al. 2001; Bischoff 2002). Along rivers this shortcoming was thought to be compensated in part by dispersal of seeds during floods (e.g., Dister et al. 1992). While fluvial seed dispersal proved to be quite successful along small, unregulated rivers (c.f. Bonn & Poschlod 1998, Boedeltje et al. 2004, Vogt et al. 2004) along large, slowly flowing rivers little is known about long distance dispersal of seeds (but Bischoff 2002).

Significance of soil seed bank

For restoration, seeds in the soil seed bank may also play an important role (c.f. Bakker et al. 1996). Although for some target species such as *Arabis nemorensis*, *Pseudolysimachion longifolium*, *Viola pumila* there were clear indications for the presence of a persistent seed bank, still the majority of rare species (e.g., *Cnidium dubium*, *Serratula tinctoria*) and of common grassland species (e.g., *Centaurea jacea*, *Ranunculus acris*) found in flood-meadows lack a persistent seed bank (Hölzel & Otte 2004a). Nevertheless, it remains unclear to what degree long persistent seeds of target species may contribute to the restoration of species-rich flood-meadows.

Microsite limitation

Even if the availability of seeds is not a limiting factor the process of establishment can only be successfully accomplished in the presence of suitable micro-sites for recruitment. Many species exhibit specific requirements for regeneration niches (Grubb 1977) that may considerably differ from those of adult plants. In this phase, coexistent vegetation can have quite diametrical impacts: while under harsh site conditions, i.e. high temperature and low soil water content, facilitation seems to be more important (Greenlee & Callaway 1996; Martinez 2003) under more favourable conditions inhibition through competition for light and water often outweighs these positive effects (Foster & Gross 1998; Lepš 1999).

In grassland on arable fields an acceleration of the development towards a closed sward may be desired to speed up the incorporation into agricultural management regimes without solely relying on subsidies. However, through increased inhibition in early stages of seedling development adequate measures, e.g., simultaneously sowing of grass, may considerably lower recruitment success of target species. While the presence of an already closed sward was found to be a major burden for the successful establishment of less competitive herbaceous species (Foster & Gross 1998; Lepš 1999; Tilman 1993), the impact of simultaneously sown grass is less clear (c.f. Bosshard 1999).

Utilisation of biomass

The task of grassland restoration is not completed, if there are no long-term concepts for adequate management. At a larger scale, management regimes solely falling back on subsidies are always prone to abatement of financial sources. Thus the first choice is to incorporate these meadows into local farming systems (Tallowin & Jefferson 1999). As in many other semi-natural grasslands of high nature conservation value, the organisation of an adequate management emerged as the main challenge in the preservation of flood meadows. The interests of farmers and conservationists are often divergent, particularly in terms of raising productivity through fertiliser application, and the date and frequency of mowing. The willingness of farmers to accept non-intensive management schemes largely depends on the quantity and quality of the biomass yield. Both aspects are of crucial importance for the marketability and utilization of the harvest as livestock fodder. While several studies have demonstrated the potential and successful incorporation of species-rich and extensively-managed meadows of mountainous and lowland regions into local farming systems (e.g., Daccord 1990; Jilg & Briemle 1993; Malcharek et al. 1998; Schellberg et al. 1999; Tallowin & Jefferson 1999), little is known about the possibilities of successfully joining interests of agriculture and nature conservation in regularly flooded alluvial meadows.

Thus the objectives of this thesis were:

i. To evaluate the potential of re-colonisation of formerly arable fields and species-impoverished grassland by rare flood-meadow species,
ii. to assess the capability of the seedbank of arable fields to contribute to the restoration of species-rich flood meadows,
iii. to evaluate the influence of different treatments possibly applied in the course of restoration measures on the process of seedling emergence and early establishment, and
iv. to assess the potential of species-rich flood-meadows to be incorporated into local farming systems and its main factors of influence.

In chapter 9, the implications of this research for the restoration of species-rich flood-meadows are discussed.

2 Main objectives

In the following, the objectives of the thesis, as listed in the preceding chapter, are presented in detail. In chapter 9, the findings of the individual studies (chapters 5-8) are discussed with respect to their implications in restoration projects.

2.1 The impact of site conditions and seed dispersal on restoration success (chapter 5)

This study deals with objective i, that is it evaluates the potential of re-colonisation of former arable fields and species-impoverished grassland by rare flood-meadow species communities, predominantly of the alliance *Cnidion*.

This was done by comparing old and new meadows with respect to floristic composition, productivity and soil conditions. The main question addressed in chapter 5 was: which differences can be found between old and newly created meadows after ten years of restoration management. Consequently, it was studied to which degree re-colonisation occurred in the area and how this process was related to the abundance of target species at remnant sites, to species traits and prevailing site conditions.

2. 2 Vegetation and seedbanks in irregularly flooded arable fields (chapter 6)

The second study treats objective ii, that is it assesses the capability of the seedbank of arable fields to contribute to the restoration of species-rich flood meadows.

After a series of dry years in the 1970s, arable use was extended even to the lowest parts of the study area (Böger 1991), which formerly held species-rich grassland. At these sites, which are only inundated by ascending ground water during long lasting floods of the River Rhine, species-rich flood meadows would be the typical grassland type. These sites were perfectly suited to evaluate the potential of the soil seed bank to contribute to the restoration of species-rich flood measows after an interim arable use. The main objectives were to analyse the floristic composition of plant communities on arable fields after drawdown of the water, the species composition and size of the seedbank and to assess its relation to above-ground vegetation, water regime and management.

2. 3 Seedling recruitment in flood meadows (chapter 7)

This study addresses objective iii, that is it evaluates the influence of different treatments, possibly applied in the course of restoration measures, on the process of seedling emergence and early establishment.

The re-colonisation of new habitats either through dispersal by remnant stands or after the active introduction of seeds from target species is strongly influenced by different prerequisites for emergence, survival and establishment. In chapter 7 the impact of simultaneously sown grass on these traits was analysed. This was done since the introduction of grasses in addition to herbaceous target species may further the incorporation of restoration sites into local farming systems and therefore has the potential to lower restoration costs. Thus the main interest was to asses, if the emergence, survival and establishment of typical flood meadow species was hampered by sown grass and whether the effects were consistent under different hydrological regimes. Additionally, the effects of litter application and disturbance on the seedling recruitment was analysed.

2. 4 Incorporation of alluvial meadows into local farming systems (chapter 8)

In this study, objective iv is dealt with, that is the potential of species-rich flood-meadows to be incorporated into local farming systems and its main factors of influence are assessed.

To accomplish this, yield and fodder quality in extensively-managed flood-meadows was investigated with respect to vegetation type, site conditions and land-use history. Additionally, the data were analysed in the light of an ongoing discussion about the possible enhancement of grassland productivity mainly by species diversity (e.g., Tilman et al. 1996; Hector et al. 1999). Thus, an additional aim of this study was to assess, whether there is a link between species-richness and nature conservation value on the one hand and productivity and fodder quality on the other hand. Beyond this, the study quantified variation in biomass yield and fodder quality between meadows of different floristic composition and nature conservation value and tried to identify the factors (site conditions, functional groups, floristic composition, species-richness) responsible for the observed differences in yield and quality.

3 Study area

The study area is situated in the Hessian part of the Holocene flood plain of the River Rhine about 30 km south-west of Frankfurt, Germany (49°51’ N, 8°23’ E; 85 m a.s.l.). It comprises several nature reserves of which the largest, i.e. NSG ‘Kühkopf-Knoblochsaue’, covers an area of 2,370 ha. The study area represents one of the last and most important strongholds of many rare and endangered alluvial grassland species, among them even species of Central European conservation concern such as *Arabis nemorensis*, *Cnidium dubium*, *Iris sibirica* and *Viola pumila* (Schnittler & Günther 1999).

The entire area is subdivided into three different hydrological compartments (Hölzel & Otte 2001):

- The functional flood-plain, riverwards the summer dykes, is directly flooded by water loaded with fine sediment during high water of the Rhine, which exhibits a maximum amplitude of more than 6 m (Dister 1980; Böger 1991).
- The hybrid flood-plain between summer and winter dykes is only flooded when the river rises 4 m above mean water level. At high river levels that do not overtop the summer dykes, ground depressions in this compartment may be submersed by ascending groundwater.
- The fossil flood-plain landwards the winter dykes is only submerged in low depressions by clear ascending, sediment-free groundwater accompanying high water levels of the Rhine.

Especially depressions are prone to the effects of indirect flooding through a rising ground-water table in the hybrid and fossil floodplain. A maximum amplitude of the ground-water table of more than 6 m is the result of the strong seasonal and inter-annual fluctuations of the water level of the River Rhine (Dister 1980; Böger 1991). In some years (e.g., 1999, 2001), winter, spring and early summer flooding may last for weeks or even months. This is an effect of the extremely fine grained (clay content > 60 %), calcareous alluvial soils topping sandy sediments of the Rhine which are predominant over the whole area and prevent a fast drainage of depressions.

The climatic conditions in the region are relatively warm and dry, with a mean temperature of 10.3 °C and a mean annual precipitation of 580 mm at the meteorological station of Worms (Müller-Westermeier 1990). In conjunction with the hydrological and edaphic conditions, the warm and dry climate results in a high variability of the soil water potential. While winter, spring and early summer may often bring floods, summers are notably dry. These conditions are similar to those prevailing along large rivers in continental eastern European lowlands, reflected by the occurrence of specialist plants of predominately subcontinental distribution such as *Allium angulosum*, *Cnidium dubium*, *Scutellaria hastifolia* and *Viola pumila*. In our study site, these species are close to the north-western limits of their areals (Hultén & Fries 1986).

Although intensified drainage started in the 1920s, species-rich alluvial grasslands that were non-intensively managed as hay-meadows were dominant in the whole area until the 1950s and even 1960s (Knapp 1954). But in the course of structural changes in agriculture and a series of dry years during the 1970s and early 1980s, arable use was increasingly extended even to the lowest parts of the area (Böger 1991). Intensified management with application of fertiliser and mowing two to three times per year further decreased species richness.

In the early 80s and 90s when most nature reserves were initiated in the area, the only large populations of target species were restricted to a few permanently non-intensively managed meadows as well as to the extensive system of drainage ditches. Beginning in the early 1980s and 1990s, about 500 ha of arable land were converted into grassland. In most cases, the former fields were sown with a species-poor seed mixture of common grasses (*Arrhenaterum elatius*, *Festuca pratensis*, *Festuca rubra*, *Poa pratensis*, *Dactylis glomerata*, *Trisetum flavescens* and *Alopecurus pratensis*), sown with freshly threshed material from species-poor and grass-dominated meadows or left to self-greening. Simultaneously, the intensity of management in the whole area was lowered by the banning of fertiliser application and the limitation of mowing to the time after mid-June. Additional efforts to enhance re-colonisation by typical and rare flood meadow species were not undertaken since the conditions for successful re-establishment of target species were regarded as sufficient to initiate and maintain the process of natural re-colonisation.

4 Methods

The following section gives an overview of the methods used for data collection and analysis.

4. 1 Sampling of above-ground vegetation - *chapters 5, 6, 8*

In the sampling of grassland vegetation, GIS was used to stratify the allotments according to the variable age (chapter 5) or floristic composition and the nature conservation value (chapter 8). According to the stratified groups, plots were evenly distributed over the entire study area and mostly placed in the central part of the sites.

To sample the above-ground vegetation in meadows, relevés of 10 by 10 m were used. Since the ephemeral wetland vegetation (chapter 6) was much more homogenous in its composition than grassland vegetation, sampling plots were only 5 by 5 m in dimension. Species abundance was estimated on a modified Braun-Blanquet-scale, which was replaced by a fully numerical 1-9 scale for the data analysis (van der Maarel 1979). Plant species nomenclature always follows Wisskirchen & Haeupler (1998).

Above-ground biomass in each 100 m^2 plot was collected by harvesting ten 0.1 m^2 squares, placed at random within the plot areas.

4. 2 Biomass analysis - *chapters 5, 8*

The collected biomass samples were dried at 105°C for 48 hours and weighed to determine the dry-matter yield (chapter 5). For the assessment of the contents of the above-ground biomass (chapter 8) the samples were dried at 60 °C for 48 hours. The NIRS (Near Infrared Reflectance Spectroscopy) method was then used (Shenk et al. 1989) to evaluate contents of crude protein, crude fibre and crude fat (chapter 8). Spectroscopy (ICP-OES; DIN EN ISO11885) was used to assess contents of phosphorus (P), calcium (Ca), sodium (Na), magnesium (Mg) and potassium (K). As measures for the energy content of the biomass, metabolizable energy (ME) as well as energy for lactation (NEL) in the case of ruminants (Kirchgeßner 1998) and digestible energy (DE) in the case of horses (DLG 1998) was calculated.

4. 3 Mapping of target species - *chapter 5*

Precise mapping was done by measuring the orthogonal distance of a single individual or group of individuals to two adjacent ditches. The obtained data were entered, further processed and analysed with the GIS software package ArcView GIS 3.2 (Anon. 1999).

4. 4 Sampling of the seedbank - *chapter 6*

Using a soil corer of 3 cm diameter, 20 cores of 10 cm depth were taken at random locations within each sampling area of above-ground vegetation after removing all plant material from the soil surface. The soil samples represent 141 cm^2 of the soil surface and 1410 cm^3 of soil volume. The seedbanks were analysed with the seedling emergence method over 30 months (cf. Roberts 1981; Hölzel & Otte 2001). After removing vegetative plant material, the soil samples were transferred to 18 cm x 28 cm Styrofoam trays as a 3 cm thick layer and exposed under free air conditions. The trays were protected against diaspore input and heating by covering them with flat, white gauze lids. Control trays filled with sterile soil were placed between the samples. Germinating seedlings were identified and removed once every week. Unidentifiable specimens were transferred to pots and grown until they could be named. When germination declined, the samples were crumbled and mixed, after removal of emerging seedlings. To quantify both the size of the seedbank of common agrestal species, regularly occurring at terrestrial sites, and the seedbank of the typical ephemeral wetland vegetation, the samples were exposed to different water regimes (cf. Ter Heerdt et al. 1999; Moravcová et al. 2001). For the first 18 month the samples were exposed to terrestrial conditions with no flooding but regular watering to keep them moist. Prior to the third season of the analysis the samples were first shallowly flooded for three months (January to March) and subsequently kept under waterlogged conditions.

4. 5 Experimental design - *chapter 8*

To analyse the effects of different treatments on seedling emergence at three sites a split-plot-design was chosen for the grass seed addition experiment and a split-split-plot design was applied to test for the effects of litter and disturbance in grassland. In both types, four replicates (blocks) were used. In case of the grass seed addition experiment different amounts of grass seeds were applied at the main plot level and the seeds of herbaceous species were sown into subplots. In case of the split-split-plot experiment in grassland, the main plots contained the disturbance variants, the sub-plots the litter treatment and at the sub-sub-plot level the herbaceous species were sown.

4. 6 Soil-nutrient analysis - *chapters 5, 8*

Collection of soil samples was carried out using a soil corer of 3 cm diameter. In each 100 m^2 plot, five cores of 10 cm depth were taken at random locations after removing living and dead plant material from the soil surface. Samples were air-dried, sieved (<2 mm) and extracted with calcium-acetate-lactate (CAL) for the determination of plant-available phosphorus (P) and potassium (K; Hoffmann 1991).

Total nitrogen (Nt) and total carbon content were analysed with an CN-Analyzer (FlashEA 1112, Thermoquest), after complete combustion of the probe at 1800°C (Anon. 2002a). Determination of the $CaCO_3$ was done according the method of Scheibler (Hoffmann 1991). Total carbon minus the $CaCO_3$-carbon gives the organic carbon in the soil. The latter was used to calculate the content of organic matter in the soil samples and the C/N-ratio, which was used as a measure for nitrogen availability (Kuntze et al. 1994).

4. 7 Data analysis

To analyse the collected data, parametric and non-parametric statistical methods as well as multivariate techniques were used. The first two were used to assess differences between groups with respect to measured variables in explorative studies or with respect to the effects of treatments applied in experimental studies. Multivariate techniques were applied to explore floristic patterns and their relation to gradients in environmental variables.

To test for differences between two groups of interest in non-normally distributed variables and variables where requirements for ANOVA were not met after data transformation, respectively, non-parametric Mann-Whitney U-test was used (e.g., old and new meadows in chapter 5, flooding treatment in chapter 6). For the analysis of normally distributed variables and variables, which could be adequately transformed (e.g., site, vegetation and forage quality parameters in chapter 8) ANOVA was applied. To analyse significant differences between several groups in detail, post hoc tests were used (e.g., Tukey´s Honest-Significance test (HSD)).

In chapter 7, ANOVA and MANOVA were used to analyse the data for significant treatment effects. While ANOVA was used to analyse the effects of treatments at single occasions in time, MANOVA was employed to include changes over time into the analyses. The reason for using MANOVA is that due to repeated counting at the same plots over two years the assumptions of ‘circularity’ and ‘compound symmetry’ were unlikely to be fulfilled (v. Ende 1993) for the within-subject factors (i.e. counting date).

Multiple regression was performed to assess the importance of populations of target species in old meadows and along ditches for the re-colonisation of new meadows in chapter 5. In all cases of correlative analysis non-parametric Spearman Rank Correlation was used (chapters 5, 6, 8).

Detrended Correspondence Analysis (DCA) was used to explore gradients in the floristic composition of vegetation samples (chapters 5, 6, 8). To reduce their influence on ordination results, rare species were omitted from the analysis. To evaluate how well the ordination distance represented the distance in the original data set, the after-the-fact evaluation was used (McCune & Grace 2002).

To test for indicator species of old and new meadows the method of Indicator Species Analysis was applied (Dufrêne & Legendre 1997; chapter 5). The indicator value of a species for one group is calculated by relating the species' mean abundance in one group with its mean abundance in all groups and multiplying the result by its relative frequency in the samples of that group.

A Mantel test (Legendre & Legendre 1998) was applied to evaluate the similarity between the seedbank and the established vegetation (chapter 6). This statistic was also used to test whether similarity was related to spatial proximity both for the vegetation samples and and for the seedbank samples from different places. The Euclidean distance measure was used to create the seedbank and vegetation matrices (i.e. analogous to the distance measure in space), but the Sørensen index was used to compare seedbank and vegetation composition.

To test for the significance of the results obtained in the analysis for indicator species and the results of the Mantel test a Monte-Carlo-permutation test was applied (McCune & Grace 2002).

5 The impact of site conditions and seed dispersal on restoration success in alluvial meadows

Tobias W. Donath, Norbert Hölzel & Annette Otte

Applied Vegetation Science 6: 13-22

5. 1 Abstract

We studied the restoration success of flood plain meadows in the northern Upper Rhine valley where, from 1988–92, 35 ha of arable land was converted into grassland and subsequently managed for nature conservation.

Remnant populations of typical alluvial meadow species were found in old meadows and along drainage ditches that dissect the whole area. We analysed the site conditions and vegetation relevés in old and new meadows. Small differences in site parameters between old and new meadows contrasted with a clear floristic differentiation between the two meadow types. The vegetation of old meadows was much more differentiated along prevailing environmental gradients than the vegetation of new meadows. Despite the favourable site conditions for the re-establishment of species-rich meadows on the former arable land, restoration success was limited to the vicinity of remnant stands. In contrast to old meadows, indicator species of new grassland were still typical species of regularly disturbed ruderal and arable habitats, often capable of building up a persistent seed bank.

The precise mapping of 23 target species revealed that even wind dispersal predominantly leads to re-establishment in the close circumference of parent plants. We found no indication that regular flooding, hay-making and autumnal grazing had an impact on re-colonisation of newly created grassland. Even under favourable conditions for the re-establishment of target species, restoration success in alluvial meadows proved to be strongly dispersal limited. We discuss the implications of our findings for future restoration management in grasslands.

Keywords: Flood-plain; Indicator species analysis; Ordination; Recruitment limitation; Rhine.

5. 2 Introduction

Suitable site conditions, especially in terms of soil nutrient status, moisture regime and the availability of seed sources either from soil seed bank or by dispersal, are regarded as basic preconditions for successful restoration management (Bakker & Berendse 1999). However, as experienced in many recent grassland restoration projects, target species and communities often do not recover, even after the soil nutrient status and the biomass production have been successfully lowered (Graham & Hutchings 1988; Bakker 1989; Berendse et al. 1992). In such cases, limited dispersal was identified as the main obstacle to restoring species-rich grasslands (Bakker et al. 1996; Hutchings & Booth 1996a; Stampfli & Zeiter 1999). Dispersal is most often hampered by spatial isolation, the lack of viable source populations of target species in the vicinity of restoration sites and the absence of traditional dispersal vectors in modern agricultural landscape (Bonn & Poschlod 1998; Muller et al. 1998; Verhagen et al. 2001; Bischoff 2002).

Along the northern Upper Rhine, large-scale restoration projects aiming at the re-establishment of species-rich alluvial meadow communities have been pursued for some 20 years (Dister et al. 1992, Hölzel et al. 2002). We studied restoration results in a flood-meadow area where, beginning in the late 1980s, arable land was transformed into grassland. While there is little hope that diaspores may have persisted in the soil seed bank after 20 years of arable use (Pfadenhauer & Maas 1987; Bakker 1989; McDonald et al. 1996; Thompson et al. 1997; Hölzel & Otte 2001), the conditions for immigration and establishment of target species from nearby sources appear favourable. Close to the restoration sites, there are large and viable populations of target species. These are either remnants in non-intensively managed species-rich alluvial meadows or populations along a system of open drainage ditches that dissects the whole area. Furthermore, dispersal should be facilitated by regular haymaking from June onwards (Strykstra et al. 1997) as well as by aftermath grazing with a large migratory flock of sheep (Fischer et al. 1996), with the latter possibly enhancing establishment (Gibson et al. 1987). Over ten years after the area was placed under protection, we expected species-enrichment at the restoration sites to be particularly successful under these favourable preconditions.

To evaluate the restoration process, in 1999 we compared old and new meadows on ex-arable land with respect to floristic composition, productivity and soil conditions. Areas that are referred to as old meadows were in the past under no arable use, while new meadows, prior to their conversion, were so at least for 20 years. Furthermore, we analysed spatial patterns of dispersal by the precise mapping of the populations of 23 target species in new and old meadows, as well as along ditches.

The questions addressed in this paper are:

1. What are the differences between old and newly created meadows in terms of floristic composition, productivity and soil properties after ten years of restoration management?
2. How successful was the re-establishment of target species, especially in relation to their abundance at remnant sites?
3. Do the distribution patterns of target species reflect individual differences in dispersal ability?
4. Is the re-establishment of target species limited by site conditions or dispersal?

5. 3 Material and Methods

Study site

The study area is situated in the Hessian portion of the Holocene flood plain of the River Rhine about 30 km south-west of Frankfurt, Germany (49°51’ N, 8°23’ E; 85 m a.s.l.). It comprises a nature reserve of 75 ha (Figure 2) that was created in 1986 to protect and re-establish species-rich alluvial grasslands. The area represents one of the last and most important strongholds of many rare and endangered alluvial grassland species, among them even species of Central European conservation concern such as *Arabis nemorensis*, *Cnidium dubium*, *Iris sibirica* and *Viola pumila* (Schnittler & Günther 1999).

The entire area is situated on the landward side of the winter dyke within 50 to 750 m of the main channel of the River Rhine. Although direct flooding is precluded, there is a considerable variation in the height of the groundwater table that may fluctuate more than 2 m per year (Böger 1991). When the Rhine is in flood, large areas in depressions are submerged by clear, ascending groundwater. In some years (e.g., 1999), winter, spring and early summer flooding may last for weeks or even months. Calcareous, extremely fine grained (clay content > 60 %) alluvial soils, topping sandy sediments of the Rhine, are predominant over the whole area. The climatic conditions in the region are relatively warm and dry, with a mean temperature of 10.3 °C and a mean annual precipitation of 580 mm at the meteorological station of Worms (Müller-Westermeier 1990). In conjunction with the hydrological and edaphic conditions, the warm and dry climate results in a high variability of the soil water potential. While winter, spring and early summer may often bring floods, summers are notably dry. These conditions are similar to those prevailing along large rivers in continental eastern European lowlands, reflected by the occurrence of specialist plants of predominately subcontinental distribution such as *Allium angulosum*, *Cnidium dubium*, *Scutellaria hastifolia* and *Viola pumila*. In our study site, these species are close to the north-western limits of their areals (Hultén & Fries 1986).

Until the 1950s (Knapp 1954) and even 1960s, species-rich alluvial grasslands that were extensively managed as hay-meadows dominated the whole area. Intensified drainage (since the 1920s), structural changes in agriculture and a series of dry years during the 1970s and 1980s accelerated the conversion of the alluvial grassland into arable fields (Böger 1991). In addition, intensified management with application of fertiliser and mowing two to three times per year further decreased species richness. In 1986, when the nature reserve (75 ha) was created, only 25 ha of grassland remained. By this time, the only large populations of target species were restricted to a few permanently extensively managed meadows as well as to the extensive system of drainage ditches. Beginning in 1988, 35 ha of arable land were converted into grassland. As this was done mostly for ornithological purposes – the area was a breeding site of the Curlew (*Numenius arquata*) – the former fields were sown with a species-poor seed mixture of common grasses (*Arrhenaterum elatius*, *Festuca pratensis*, *Festuca rubra*, *Poa pratensis*, *Dactylis glomerata*, *Trisetum flavescens* and *Alopecurus pratensis*) or with freshly threshed material from species-poor and grass-dominated meadows. Simultaneously, the intensity of management in the whole area was lowered by the banning of fertiliser application and the limitation of mowing to the time after mid-June.

Additional efforts to enhance vegetation diversity, for example the transfer of diaspores with litter (Patzelt & Pfadenhauer 1998), were not undertaken, since the conditions for successful re-establishment of target species were regarded as sufficient to initiate and maintain the process of natural re-colonisation.

Sampling of vegetation

Using GIS, the allotments were stratified according to the variable age (old and new). In each group 21 plots were evenly distributed over the entire area, placing them usually in the central part of an allotment. There was a slight bias between new and old meadows with respect to the height above groundwater table, owing to the fact that higher and therefore drier meadows were preferentially converted into arable fields.

Composition of vascular plant species was sampled in plots (10 x 10 m) in June 1999. Species abundance was estimated on a modified Braun-Blanquet-scale (with cover degree 2 subdivided into 2m, 2a and 2b), which for the data analysis was replaced by a fully numerical 1-9 scale (van der Maarel 1979). Plant species nomenclature follows Wisskirchen & Haeupler (1998). As an integrative measure of productivity, above-ground biomass in each 100 m^2 plot was collected by harvesting ten 0.1 m^2 squares, placed at random within the plot areas. The biomass samples were dried at 105°C for 48 hours to determine the dry-matter yield.

Soil-nutrient analysis

Collection of the soil samples was carried out using a soil corer of 3 cm diameter. In each 100 m^2 plot, five cores of 10 cm depth were taken at random locations after removing living and dead plant material from the soil surface. Samples were air-dried, sieved (<2 mm) and extracted with calcium-acetate-lactate (CAL) for the determination of plant-available phosphorus (P) and potassium (K; Hoffmann 1991).

Total nitrogen (Nt) and total carbon content were analysed with an CN-Analyzer (FlashEA 1112, Thermoquest), where after complete combustion of the probe at 1800°C the C- and N-content in the gas is measured (Anon. 2002). Determination of the $CaCO_3$ was done according the method of Scheibler (Hoffmann 1991). Total carbon minus the $CaCO_3$-carbon gives the organic carbon in the soil. This was used to calculate the content of organic matter in the soil samples and the C/N-ratio, which was used as a measure for nitrogen availability (Kuntze et al. 1994).

Mapping of target species

To analyse the re-colonisation of the ex-arable land by plants in greater detail, we precisely mapped the populations of 23 target species (species listed in Figure 2). These are all species which are considered as threatened or in decline in Europe, Germany or Hesse (Buttler et al. 1996; Korneck et al. 1996; Schnittler & Günther 1999). Precise mapping was done by measuring the orthogonal distance of a single individual or group of individuals to two adjacent ditches. The obtained data were entered, further processed and analysed with the GIS software package ArcView GIS 3.2 (Anon. 1999).

Data analysis

To test for differences in site and vegetation parameters between old and new meadows, we used the non-parametric Mann-Whitney-Test. To keep the global type I error at 5 % despite multiple testing, the significance level α was adjusted by a modified Bonferroni procedure (Holm 1979). From vegetation samples, we derived cover-weighted means of the Ellenberg values for moisture, nutrients and soil-reaction (Ellenberg et al. 1991). Correlations between environmental variables were analysed by non-parametric Spearman Rank Correlation.

Detrended Correspondence Analysis (DCA) was used to explore gradients in the floristic composition of vegetation samples. To reduce their influence on ordination results, species with less than three occurrences were omitted from the analysis, which meant a reduction from 116 to 75 species. No further data transformation was carried out. To evaluate how well the ordination distance represents the distance in the original data set, we used the after-the-fact evaluation (McCune & Mefford 2002). Correlations between a subset of site and vegetation parameters and the DCA sample scores were analysed by Spearman Rank Correlation. Additionally, we performed separate DCAs of old (N=21) and new meadows (N=20), to analyse potential differences in the total inertia. One extreme sample of the new meadows was excluded.

Significant indicators of old and new meadows were detected by the method of Indicator Species Analysis (Dufrêne & Legendre 1997). To calculate the indicator value of a species, its mean abundance in one group compared with its mean abundance in all groups is multiplied by its relative frequency in the samples of that group. The obtained values were tested for significance with a Monte-Carlo-Permutation test (5000 permutations).

Multiple regression was performed to assess the importance of populations of target species in old meadows and along ditches (explanatory variable) for the re-colonisation of new meadows (dependent variable). While in the first model, the impact of the number of species in adjacent old meadows and along ditches on the number of species in the new meadows was analysed, the second model analysed the influence of all subpopulations of a species within old meadows and along ditches on the re-colonisation of new meadows. In the second model, variables were log-transformed prior to data analysis for normalisation.

The statistical analyses and correlations were all performed with the software package STATISTICA 5.1 (Anon. 1998). DCA, Indicator Species Analysis and the related statistical verifications were done with PC-Ord 4.14 (McCune & Mefford 1999).

5. 4 Results

Comparison of old and new meadows

The comparison of site-related traits revealed significant differences between new and old meadows, with respect to organic matter content, total nitrogen, plant available P, biomass yield, total coverage and the mean Ellenberg values for moisture, which were all higher in old meadows (Table 1). In contrast, only plant-available K displayed a significantly higher value in new meadows. In all other traits there were no significant differences between old and new meadows.

Table 1. Statistical tests (Mann-Whitney Test) for differences in site and vegetation parameters between old and new meadows. Significant differences at Bonferroni-Holm adjusted α (Holm 1979) are indicated by an asterisk after the corresponding *P*. *x* = mean; *sem* = standard error of the mean.

	Old meadows		New meadows		*P*	Bonferroni-Holm
	x	*Sem*	*x*	*sem*		adjusted α
Organic matter in soil (%)	12.45	0.61	7.79	0.35	< 0.001 *	0.0042
Total nitrogen (%)	0.69	0.03	0.44	0.02	< 0.001 *	0.0045
Phosphorus (mg/100g)	14.52	0.63	11.09	0.5	< 0.001 *	0.005
Ellenberg moisture value	6.0	0.15	5.3	0.1	< 0.001 *	0.0056
Coverage (%)	94.0	1.81	88.95	1.37	< 0.001 *	0.006
Potassium (mg/100g)	9.03	0.24	10.31	0.29	0.002 *	0.007
Biomass yield (g/m^2)	729.05	32.44	588.67	23.66	0.003 *	0.008
C/N-Ratio	10.55	0.09	10.30	0.08	0.012	0.01
Species number	23.6	1.21	26.90	1.18	0.066	0.013
Ellenberg reaction value	6.9	0.05	6.9	0.1	0.163	0.017
Ellenberg nutrient value	5.8	0.08	5.6	0.09	0.187	0.025
$CaCO_3$ (%)	12.69	1.13	13.31	0.77	0.458	0.05

Table 2. Correlation coefficients (Spearman rank correlation) between site and vegetation parameters. Age is a binary variable coded with 0 for old and 1 for new meadows. The significance is indicated at three levels of α: * ≤ 0.05, ** ≤ = 0.01, *** ≤ 0.001. Coefficients of correlation ≥ 0.5 are in bold. Units as given in table 1.

Variable	Age	Species number	Coverage	Biomass	Moisture value	Nutrient value	Reaction value	Phos-phorus	Potassium	Total nitrogen	$CaCO_3$	C/N
Age	1											
Species number	0.29	1										
Coverage	**-0.54*****	0.10	1									
Biomass yield	-0.47**	-0.22	**0.51*****	1								
Moisture value	**-0.55*****	-0.21	0.34*	**0.55*****	1							
Nutrient value	-0.21	-0.27	0.2	0.23	0.31*	1						
Reaction value	0.22	0.09	-0.07	0.06	0.02	-0.32*	1					
Phosphorus	**-0.55*****	-0.34*	0.27	0.40**	0.37*	0.25	0.17	1				
Potassium	0.49***	0.29	-0.10	-0.27	**-0.53*****	-0.11	-0.16	-0.29	1			
Total nitrogen	**-0.78*****	-0.13	0.37*	0.44**	**0.68*****	0.13	0.27	**0.55*****	**-0.64*****	1		
$CaCO_3$	0.12	-0.19	-0.13	0.12	0.28	-0.03	-0.24	-0.23	-0.31*	0.12	1	
C/N-ratio	-0.39*	-0.03	0.42**	0.24	0.34*	0.09	-0.06	0.11	-0.19	0.22	0.07	1
Organic matter	**-0.80*****	-0.14	0.41**	0.45**	**0.66*****	0.16	0.26	**0.54*****	**-0.65*****	**0.97*****	0.10	0.37*

Since age is a binary variable, in this context coded as 0 for old and 1 for new meadows, a positive correlation between age and a variable implies higher values of that variable in new meadows and vice versa. The correlation matrix in Table 2 confirmed a strong correlation between the above-mentioned traits and the variable age, which resulted in many further correlations between site and vegetation variables.

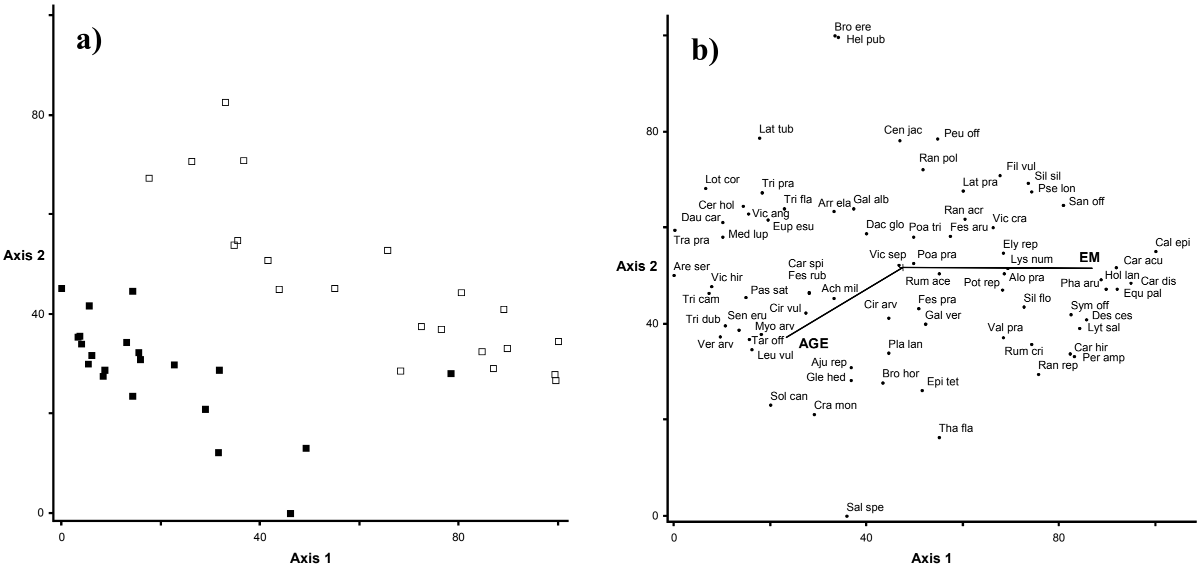

Figure 1. DCA ordination diagrams. a): scores of all relevés along axes 1 and 2. Filled squares represent new meadow and empty squares old meadow relevés. b): Joint plot (axes 1 and 2) of DCA scores of all species with more than two occurrences and the vectors of age (old = 0; new = 1) and the Ellenberg moisture value (EM). Full species names are given in the appendix at the end of this paper.

DCA ordination revealed a total inertia of 1.878. The first axis had the highest eigenvalue (0.40), while the eigenvalues of axis 2 and 3 (0.13 and 0.08 respectively) indicated their minor importance. The gradient lengths of the first and second axis both exceeded 2 standard deviation units (2.466 and 2.036 respectively). The after-the-fact evaluation indicated that most of the variance in the original dataset was already accounted for by the first axis ($R^2 = 0.744$), while the second and third axis contributed only about 0.05 each.

The DCA ordination plot (Figure 1a) displayed a clear separation of old and new meadows along the first and second axis, with the exception of one relevé from a new meadow which was grouped along with the old meadows. New meadows were much more aggregated in ordination space, while old meadows showed a much wider scatter.

Table 3. Correlation coefficients (Spearman rank correlation) between sample scores on the first two DCA axes of full data set, site and vegetation variables. The significance is given at three levels of α: * ≤ 0.05, ** ≤ 0.01, *** ≤ 0.001. Coefficients of correlation ≥ 0.5 are in bold. Units as given in table 1. N = number of included relevés.

	All samples (N=42)	
	Axis 1	Axis 2
Age	**-0.72*** **	**-0.52*** **
Phosphorus	0.47**	0.23
Potassium	**-0.67*** **	-0.01
C/N	0.14	0.14
Moisture value	**0.82*** **	-0.09

The first axis of DCA displayed a fairly strong correlation with the environmental variables age, P, K and the mean Ellenberg value for moisture, while there was no correlation with the C/N-value (Table 3). Age was the only variable that loaded fairly strong on axis 2. Running a DCA on old and new meadows separately revealed an inertia of 0.893 for new meadows and a higher inertia of 1.408 for old meadows, which corresponds to their pattern in Figure 1a. Only in the case of the old meadows, the gradient length of the first axis was above 2 standard deviations, while for the new meadows the gradient length for all axes was below this value.

Table 4 shows the species typical of old and new meadows that had a significant indicator value of at least 25 according to the method of Dufrêne and Legendre (1997).

Distribution patterns of target species

The precise mapping of plant populations over the entire nature reserve revealed a high concentration of target species in old meadows and along ditches (Figure 2). In contrast, there were few occurrences of target species in newly created meadows, and most of these were directly connected to neighbouring source populations in old meadows and along ditches. Multiple regression (Table 5) showed that the number of target species in new meadows was only significantly dependent on their occurrence along ditches but not in old meadows. This pattern did not change but explained

Table 4. Indicator Species of old and new meadows. The significance obtained by the Monte-Carlo-Permutations Test is given at three levels: * ≤ 0.05, ** ≤ 0.01, *** ≤ 0.001. ° indicates that species produces seeds with pappi which are therefore wind-dispersed. IV = Indicator Value in percent; SBT = Seed-Bank-Type according to Thompson et al. (1997) and Grime et al. (1988) [1 = transient, 2 = short-term persistent, 3 = long-term persistent]; LF = Life Form according to Grime et al. (1988) and Schiefer (1980); AW = common Arable Weeds in the study area; n. m. = not mentioned.

	IV	SBT	LF	AW
Old meadows				
Sanguisorba officinalis	76.2***	1	H	
Lathyrus pratensis	63.4**	2	H	
Alopecurus pratensis	59.4**	2	H	
Festuca arundinacea	57.6**	2	H	
Carex acutiformis	50.1***	2	H	
Vicia craca	49.0*	1	H	
Agropyron repens	46.6*	2	H	x
Symphytum officinale	43.2**	1	H	
Carex disticha	42.9**	2	H	
Potentilla reptans	40.3*	3	H	
Peucedanum officinale	40.0**	n. m.	H	
Ranunculus acris	35.7*	3	H	
Holcus lanatus	35.6**	3	H	
Phalaris arundinacea	35.3*	3	H	
Calamagrostis epigejos	28.6*	2	H	
New meadows				
Leucanthemum vulgare	90.5***	3	H	
Taraxacum officinale°	73.3***	3	H	x
Festuca rubra	66.7***	1	H	
Cirsium arvense°	65.1***	3	G	x
Trisetum flavescens	61.1***	1	H	
Vicia angustifolia	60.5***	3	Th	x
Achillea millefolium	59.4**	2	Ch	x
Senecio erucifolius°	58.6***	n. m.	H	
Trifolium campestre	54.5***	1	Th	x
Poa pratensis	53.8*	3	H	
Pastinaca sativa	51.1**	3	H	
Vicia hirsuta	47.6***	3	Th	x
Solidago canadensis°	42.9***	1	H	x
Crataegus monogyna	42.9**	1	Ph	
Bromus hordeaceaus	41.7**	2	Th	x
Ajuga reptans	39.7*	3	H	
Cerastium holosteoides	38.4*	3	Ch/Th	x
Myosotis arvensis	37.5*	3	Th	x
Veronica arvensis	33,3*	3	Th	x
Medicago lupulina	29.6*	3	Th/H	x

variance was even higher when the number of subpopulations and individuals of each species in the old meadows and along ditches was used in the regression model.

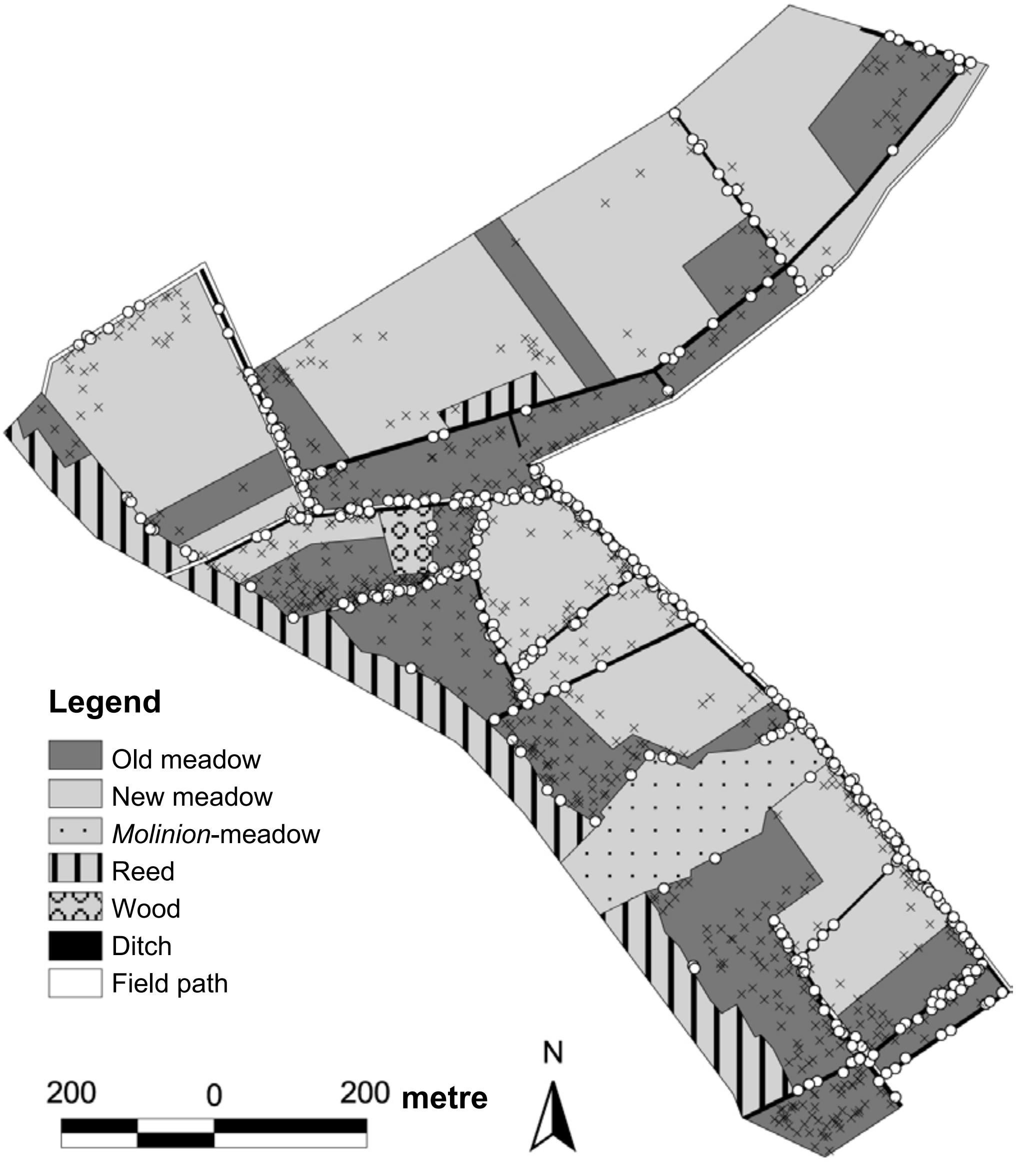

Figure 2. Distribution of target species in the study area. Individuals/subpopulations of target species along ditches are identified by circles, in meadows by crosses. List of the target species, the number of their occurrences is given in brackets: *Allium angulosum* (18), *Arabis nemorensis* (7), *Carex praecox* (59), *Carex tomentosa* (78), *Cirsium tuberosum* (87), *Cnidium dubium* (1), *Dianthus superbus* (1), *Euphorbia palustris* (27), *Fillipendula vulgaris* (13), *Galium boreale* (19), *Gentiana pneumonanthe* (1), *Inula britannica* (2), *Inula salicina* (48), *Iris sibirica* (2), *Lathyrus palustris* (19), *Peucedanum officinale* (239), *Primula veris* (191), *Pseudolysimachion longifolium* (43), *Scutellaria hastifolia* (4), *Serratula tinctoria* (9), *Tetragonolobus maritimus* (5), *Thalictrum flavum* (47), *Viola pumila* (2).

Table 5. Statistics of the multiple regression models with the number of target species and the number of individuals/subpopulations in new meadows as the respective dependent variable (y). In the second model the variables are the number of occurrences of each species in the three habitats; both dependent (y) and explanatory (x) variables are log-transformed. The parameter estimates of the explanatory variables are standardised and *P* gives the *P*-Value of the t-test for their deviation from zero. R^2 is the variance explained by the model. The right-hand side gives the ANOVA table for the regression models. df = Degrees of freedom; MSQ = Mean Squares; *P* gives the *P*-Value of the global F-test for the deviation of the parameter estimates from zero.

Multiple regression				ANOVA			
Variable	Parameter estimate	*P*	R^2	Source	df	MSQ	*P*
Number of target species in new meadow - y			0.49				
Intercept	0.05	0.95		Regression	2	33.42	<0.001
Species per neighbouring meadows - x	0.25	0.135		Residual	24	2.46	
Species per adjacent ditches/paths - x	**0.56**	0.002					
Number of subpopulations in new meadows - log(y)			0.58				
Intercept	-0.09	0.50		Regression	2	2.45	<0.001
Subpopulations in old meadows - log(x)	0.32	0.07		Residual	20	0.15	
Subpopulations along ditches/paths - log(x)	**0.56**	0.003					

For three species, the minimum range of dispersal and establishment during the last 10 years is given in Figure 3. Dispersal was analysed in areas where the occurrences in new meadows were clearly linked to source populations along adjacent ditches. The wind-dispersed C*irsium tuberosum* proved to be the most successful species with maximum dispersal distances of more than 50 m. Maximum dispersal distances were much lower for *Carex tomentosa* and *Peucedanum officinale* with 20 and 13 m, respectively. However, the median dispersal distance of *Cirsium* was only 6 m within 10 years, while the values of *Carex tomentosa* and *Peucedanum officinale* were much lower with 1 to 4 m, respectively.

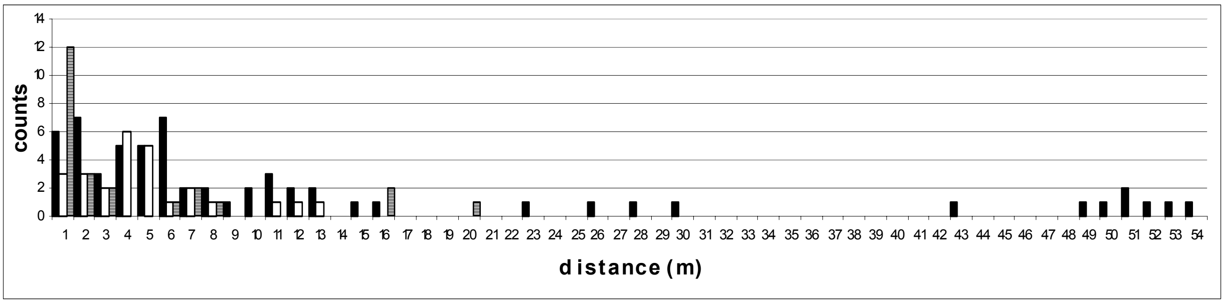

Figure 3. Minimum dispersal and establishment distances of *Cirsium tuberosum* (black), *Peucedanum officinale* (white) and *Carex tomentosa* (hatched) since 1992. The number of individuals of each species in new meadows is plotted against their distance to the closest ditch with occurrence of the respective species.

5. 5 Discussion

Comparison of old and new meadows

In general, low nutrient supply is regarded as a crucial premise for species re-establishment. In our study, N_t and plant available P had significantly higher levels in species-rich old meadows and only K was higher in the former arable areas (Table 1). Non-significant differences of C/N-ratio as a measure for the plant availability of nitrogen and of the mean Ellenberg nutrient values suggest that the level of nitrogen supply in both types of meadows is very close, if not the same. Thus, differences in the vegetation should not result from differences in nitrogen availability. Various studies on the influence of nutrient availability on species richness in different grassland types suggest a dependency of species richness mainly on low P availability (Gough & Marrs 1990; Tallowin & Smith 2001) or low P availability in combination with low K availability (Oomes et al. 1996; Critchley et al. 2002). Comparing the obtained levels of plant-available P and K with nutrient content classes used in agricultural grassland management to specify the needed quantity of fertiliser shows that only the contents of plant available P are strongly raised in both meadow types (Table 6). This shows that the nutrient availability is raised in both meadow types and the differences therefore do not seem to be sufficiently relevant to explain the serious floristic differences found. Another factor that puts the different nutrient levels into perspective is the low water supply, especially during summer months, which also lowers the nutrient availability in both meadow types. Additionally, the measures for prevailing competition, biomass yield and ground cover, which are lower in new meadows, add to the favourableness of new meadows for seedling emergence and establishment.

Table 6. Nutrient content classes used in agricultural grassland management for plant available phosphorus and potassium in meadows; capital letters indicate the degree of fertilisation needed to sustain mean biomass yields: A = strongly raised fertilisation, B = slightly raised fertilisation, C = moderate fertilisation to sustain productivity, D = reduced fertilisation, E = no fertilisation (Anon. 1993).

	A	B	C	D	E
Phosphorus (mg/100g)	0 - 2.7	2.8 - 6.3	6.4 - 11.2	11.3 - 17.3	17.4 -
Potassium (mg/100g)	0 - 5.3	5.4 - 12.0	12.1 - 21.3	21.4 -32.8	32.9 -

In our study, we have found two contrasting floristic trends. The total species number was significantly higher in the new meadows, the result of a higher abundance of ruderal and agrestial species which, in our case, are of no conservational interest. However, target species are still found in higher numbers and abundance in old meadows (Figure 2).

These floristic differences reappear in the DCA-plot, revealing a clear and strong differentiation between new and old meadows (Figure 1a) with the variable age showing a high correlation to the sample scores of the first two DCA-axis (Table 3). The old meadow relevés are arranged in the upper right half and show a wide scatter, owing to their higher differentiation. In contrast, the new meadow samples are clumped together in the lower left half. These distributions, in combination with the high loading of the Ellenberg moisture value on the first axis, suggest that the differentiation of the vegetation in the new meadows did not reach the level of the old meadows. The missing differentiation in the vegetation in new meadows is also strongly revealed in the DCAs of the subsets with the total inertia in old meadows being substantially higher than in new meadows (1.408 compared to 0.893). Only when remnant populations of typical meadow species are in close proximity is the vegetation at those sites already invaded by these species and reaches higher resemblance to old meadows at similar sites. This link becomes obvious in the DCA-plot with the one new meadow relevé which is grouped along with the old ones and is located only 2 m from a ditch.

The correlations of the site variables P, K and the mean Ellenberg moisture value with the sample scores (Table 3) are mainly caused by their correlation with the variable age (Table 2). Moreover, the differences in the mean Ellenberg moisture values (0.69) are too small to assume a relevant moisture gradient between old and new meadows. In fact, the bias between old and new meadows with regard to their elevation is hardly revealed in the vegetation differences between the groups.

Differences between old and new meadows were obvious with regard to the biological traits of their indicator species (IS). While old meadows were floristically well characterised along a predominant moisture gradient, ranging from species of drier (e.g., *Bromus erectus*, *Centaurea jacea*, *Peucedanum officinale*) to those of wet sites (e.g., *Persicaria amphibia*, *Ranunculus repens*, *Lythrum salicaria)*, new meadows lacked such a clear floristic differentiation (Figure 1b). In contrast, a great number of ruderals and weeds were still characteristic for new meadows. As a rule, IS of old meadows were perennial hemicryptophytes, half of them grasses and sedges with predominantly vegetative means of dispersal (Table 4). The latter may explain why different distances from remnant sites lead to a differentiation in the group of new meadows as seen in DCA ordination. None of these species have special adaptations for wind-dispersal, and most of them have been categorised as species with transient or short term persistent seedbank (Thompson et al. 1997). Both traits are regarded as important characteristics for re-establishment. In contrast, IS of new meadows were mostly typical species of regularly disturbed ruderal and arable habitats, many of them therophytes capable of forming a long term persistent soil seed bank. Their occurrence highlights the still open canopy and not fully developed vegetation in the new meadows. There were several wind-dispersed species among the indicator species of new meadows, such as *Taraxacum officinale agg.*, *Senecio erucifolius* and *Solidago canadensis*. Most of the already well-established meadow grasses are remnants of the seed mixture, which was used to enhance the development of grassland.

Distribution patterns of target species

The wind-dispersed *Cirsium tuberosum* was the most successful target-species with a maximum bridged distance of more than 50 m, while the other two species investigated, *Carex tomentosa* and *Peucedanum officinale*, reached only one fifth of this value (Figure 3). However, these differences were much less obvious when the median bridged distances was considered, which was well below 10 m for all three species. For *Silaum silaus* and the wind-dispersed *Serratula tinctoria* Bischoff (2002) found up to 77 % of the emerging seedlings within a 1.5 m radius of the parent plants. Field experiments with ten different *Apiaceae* showed for species with nearly the same height as *Peucedanum officinale* (i. e. *Heracleum sphondylium*, *Angelica sylvestris*) only a median seed-dispersal distance of about 2 to 3 m (Jongejans & Telenius 2001). In the northern part of the study area, there were singular occurrences of non-wind-dispersed target species such as *Carex tomentosa*, *Primula veris*, *Thalictrum flavum* at greater distances from potential parent plants. Remarkably, all these species are known to build up a long term persistent seed bank (Fischer 1987; Thompson et al. 1997). The probable emergence of these species from soil seed bank is supported by their distribution patterns in certain areas without contact to remnant populations. Since re-establishment mostly occurred in close proximity to remnant sites, our data does not support the occurrence of seed dispersal over greater distances by hay-making, flooding or sheep-grazing on a regular basis. In contrast, the positive effect of remnant populations at the outskirts of restoration sites was clearly reflected by the distribution patterns of the target species in new meadows. In the more diversified southern part of the study area, with a high number old meadows and ditches with source populations the invasion of new meadows was substantially higher. The importance of source populations close to restoration grassland is underlined by the result of the regression. Both, the number of target species and the number of subpopulations of each species found in new meadows was significantly related only to their counterparts along ditches. Hence, even the higher numbers of individuals in the old meadows which suggest a more intense seed rain and consecutively an increasing probability of seeds arriving at safe sites (Harper 1977), do not seem to compensate for the on average longer dispersal distances to the new meadows. This effect may be intensified by lines of bushes and trees around species-rich old meadows that may cause spatial isolation.

Conclusions for restoration management

Our study showed that suitable abiotic site conditions are no guarantee of restoration success. As in other studies, dispersal limitation of target species was revealed as the most seriously limiting factor. Viable remnant populations of target species in the vicinity of restoration sites proved to be of major importance for species-enrichment at the target sites. However, even under favourable conditions, dispersal and establishment of target species seems to be an uncertain and time-consuming process. Management of remnant populations and target areas, time and active enhancement of seed dispersal are the main agents that strongly influence restoration success in terms of species enrichment. Therefore management has to be adjusted with the aim of keeping viable populations of target species, as the only substantial local seed sources of certain target species, at neighbouring remnant sites especially giving them the opportunity to reproduce. In particular, since small and fragmented remnant populations along linear structures such as ditches are often threatened by abandonment and other adverse influences (e.g., eutrophication) as well as by stochastic events or altered population dynamics (e.g., Oostermeijer et al. 1994; Fischer & Matthies 1998).

Beside seed limitation densely closed canopy structures may be another limiting factor in grassland restoration. While annuals and other short lived ruderals dominating early successional stages are usually not hampering the reestablishment of introduced target-species (Bosshard 1999; Pfadenhauer & Miller 2000) several experimental studies clearly revealed a negative impact of closed swards on seedling recruitment (Gross & Werner 1982; Goldberg & Werner 1983; Kotorová & Leps 1999). Thus, a delayed introduction of grasses would widen the temporal and spatial extent of the “regeneration niche” (Grubb 1977) and give target species a temporal edge in establishment (“initial floristic composition” sensu Egler 1954). To prolong this period with favourable recruitment conditions is of high practical relevance since subsequent measures to create a more open sward such as grubbing and sod cutting are cost intensive and may harm already established target-species. Furthermore, such measures are usually fraught with low acceptance by land-owners and farmers.

As shown by the distribution patterns of the target species, re-establishment from adjacent remnant populations is in principle possible and successful but species mostly bridged very short distances within a period of ten years. Traditional agricultural dispersal processes, such as haymaking and aftermath grazing, alone do not seem to be very effective under present-day conditions. To shorten the time period until widespread re-establishment occurs by itself, supplementary measures such as the sowing of seeds (e.g., Bosshard 1999) or the transfer of diaspores with plant material from species-rich source stands (e.g., Patzelt et al. 2001) seem to be most promising. Judging from our results and comparable studies (Verhagen et al. 2001; Bischoff 2002), such measures are indispensable at restoration sites where remnant populations of target species disappeared completely in the close surroundings.

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Appendix

List of abbreviated species names used in Figure 1b and their full names according to Wisskirchen & Haeupler (1998).

Abbreviation	Full name	Abbreviation	Full name
Ach mil	*Achilea millefolium agg.*	Lyt sal	*Lythrum salicaria*
Aju rep	*Ajuga reptans*	Med lup	*Medicago lupulina*
Alo pra	*Alopecurus pratensis*	Myo arv	*Myosotis arvensis*
Are ser	*Arenaria serpyllifolia agg.*	Pas sat	*Pastinaca sativa*
Arr ela	*Arrhenaterum elatius*	Per amp	*Persicaria amphibia*
Bro ere	*Bromus erectus*	Peu off	*Peucedanum officinale*
Bro hor	*Bromus hordeaceaus*	Pha aru	*Phalaris arundinacea*
Cal epi	*Calamagrostis epigejos*	Pla lan	*Plantago lanceolata*
Car acu	*Carex acutiformis*	Poa pra	*Poa pratensis agg.*
Car dis	*Carex disticha*	Poa tri	*Poa trivialis*
Car hir	*Carex hirta*	Pot rep	*Potentilla reptans*
Car spi	*Carex spicata*	Pse lon	*Pseudolysimachion longifolium*
Cen jac	*Centaurea jacea*	Ran acr	*Ranunculus acris*
Cer hol	*Cerastium holosteoides*	Ran pol	*Ranunculus polyanthemos agg.*
Cir arv	*Cirsium arvense*	Ran rep	*Ranunculus repens*
Cir vul	*Cirsium vulgare*	Rum ace	*Rumex acetosa*
Cra mon	*Crataegus monogyna s. l.*	Rum cri	*Rumex crispus*
Dac glo	*Dactylis glomerata agg.*	Sal sp	*Salix spec.*
Dau car	*Daucus carota*	San off	*Sanguisorba officinalis*
Des ces	*Deschampsia cespitosa*	Sen eru	*Senecio erucifolius*
Ely rep	*Elymus repens*	Sil flo	*Silene flos-cuculi*
Epi tet	*Epilobium tetragonum s. l.*	Sil sil	*Silaum silaus*
Equ pal	*Equisetum palustre*	Sol can	*Solidago canadensis*
Eup esu	*Euphorbia esula*	Sym off	*Symphytum officinale s. l.*
Fes aru	*Festuca arundinacea*	Tar off	*Taraxacum officinale agg.*
Fes pra	*Festuca pratensis s. l.*	Tha fla	*Thalictrum flavum*
Fes rub	*Festuca rubra agg.*	Tra pra	*Tragopogon pratensis s. l.*
Fil vul	*Filipendula vulgaris*	Tri cam	*Trifolium campestre*
Gal alb	*Galium album*	Tri dub	*Trifolium dubium*
Gal ver	*Galium verum agg.*	Tri fla	*Trisetum flavescens*
Gle hed	*Glechoma hederacea*	Tri pra	*Trifolium pratense*
Hel pub	*Helictotrichon pubescens*	Val pra	*Valeriana pratensis*
Hol lan	*Holcus lanatus*	Ver arv	*Veronica arvensis*
Lat pra	*Lathyrus pratensis*	Vic ang	*Vicia angustifolia*
Lat tub	*Lathyrus tuberosus*	Vic cra	*Vicia cracca agg.*
Leu vul	*Leucanthemum vulgare agg.*	Vic hir	*Vicia hirsuta*
Lot cor	*Lotus corniculatus*	Vic sep	*Vicia sepium*
Lys num	*Lysimachia nummularia*		

6 Ephemeral wetland vegetation in irregularly flooded arable fields along the northern Upper Rhine: the importance of persistent seedbanks

Stephanie Bissels, Tobias W. Donath, Norbert Hölzel and Annette Otte

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6. 1 Abstract

Along the northern Upper Rhine ephemeral wetland vegetation is not confined to primary habitats such as the fringes of backwaters and river banks, but is also found in irregularly flooded arable fields. Within these highly variable environments, where disturbance is not only by flooding but also by agricultural management, we assessed the role of seedbanks for the persistence of ephemeral vegetation. In order to achieve this, we analysed the floristic composition of the above-ground vegetation and the corresponding soil seedbank of arable fields after a long-lasting spring and early summer flood in 2001. Moreover, we compared our vegetation data with other phytosociological studies from primary and secondary habitats along the northern Upper Rhine.

The comparison between primary and secondary habitats of mudflat species revealed differences in species composition. While primary habitats were characterised by the predominance of species of Isoëto-Nanojuncetea and Bidentetea, secondary habitats contained additionally species of the classes Agrostietea and Stellarietea.

The studied soil seedbanks were dominated by species typical of both, mudflat and agricultural habitats. Most species found in the seedbank were characterised by short life cycles and the ability to rapidly exploit periods of favourable conditions for germination and growth. The flooding treatments that were applied prior to the third season of seedbank analysis almost generally resulted in a high proportion of additional germination of mudflat species, even two years after the start of the analysis. The emergence of some mudflat species such as *Gnaphalium uliginosum*, *Veronica peregrina* and semi-aquatic helophytes such as *Alisma lanceolatum* and *A. plantago-aquatica* was actually confined to the flooding treatment.

Seed densities were exceptionally high and increased with the duration and frequency of inundation at the sampling sites. *Juncus bufonius*, *Ranunculus sceleratus* and *Veronica catenata* were the most abundant species. For *Juncus bufonius* we found a maximum seed density of 707,072 seeds*m^{-2}, which is to our knowledge the highest seed concentration that was ever found in a higher plant. The large persistent soil seedbanks proved to be of outstanding importance for the emergence of ephemeral wetland vegetation after flood disturbances in arable fields. This was also reflected by the relatively high similarity between the seedbank and the established vegetation directly after flooding.

Our study highlights the importance of irregularly flooded arable fields as a secondary habitat for the conservation of ephemeral wetland species. At these sites, not only improved drainage and landfill threatens the occurrence of mudflat vegetation but also the replenishment of the seedbank is often prevented by early re-ploughing of the fields.

Keywords: Floodplain, Germination, Inundation, Isoëto-Nanojuncetea, Mudflat vegetation.

6. 2 Introduction

In riverine wetlands strong seasonal and interannual fluctuations of the water level may cause distinct vegetation dynamics along elevational gradients. Extended inundation at higher elevation that leads to a complete or partial dieback of the established canopy as well as periods of drought that create mudflats at the fringes of water bodies are typical situations that provide temporary suitable conditions for ephemeral wetland vegetation (Abernethy & Willby 1999). Due to the irregularity and unpredictability of such events persistent soil seedbanks play an important role along lowland rivers and largely determine the vegetation directly after drawdown. Thus, most ephemeral mudflat species are well known to build up large persistent soil seedbanks and are able to germinate directly after drawdown (van der Valk & Davis 1978; Casanova & Brock 2000; Jutila 2001). Beyond this, mudflat species have to rapidly complete their lifecycle and to refill the seedbank before the vegetation dies off when the soil dries out, succession proceeds or another disturbance occurs.

There are numerous studies on seedbanks of temporary marshes and tidal freshwater wetland (van der Valk & Davis 1978; Leck & Graveline 1979; Smith & Kadlec 1983; Ter Heerdt & Drost 1994; Leck & Simpson 1995). Contrary, relatively little information exists about the seedbanks of riverine wetlands (Schneider & Sharitz 1986; Abernethy & Willby 1999; Goodson et al. 2001, 2002), and about mudflat vegetation of secondary habitats in particular. While seedbank analysis of temporarily drained ponds were conducted by, e.g., Poschlod et al. (1996), seedbank studies of ephemeral wetland vegetation in secondary habitats along rivers are completely missing. Low-lying arable fields landwards the dykes constitute such secondary habitats along the northern Upper Rhine. An early description of the floristic composition of ephemeral plant communities in this particular situation was given by Oesau & Froebe (1972). This study revealed that irregularly flooded arable fields along riparian corridors comprise an important but so far neglected secondary habitat of ephemeral wetland vegetation. Presently, we have little knowledge whether agricultural intensification and changes in hydrology may adversely influence the persistence of these habitats. In this context long-term persistent soil seedbanks must be considered as a key factor to ensure the survival of mudflat species over periods of intense arable use.

In the present study we recorded the ephemeral mudflat vegetation in arable fields in the floodplain of the northern Upper Rhine and analysed the role of the seedbanks in this habitat. All fields were situated on the landward site of high winter dykes (fossil floodplain) and lower summer dykes (hybrid floodplain), respectively. However, during high water levels of the Rhine shallow depressions in all fields under study are inundated by ascending, clear and sediment-free groundwater and in the hybrid floodplain also by high floods that spill over the low summer dykes. The subsequent drawdown leads to germination and establishment of mudflat species in open patches of the arable fields where a dieback of the crop has taken place during flooding.

The main objectives of this study were i) to analyse the floristic composition of mudflat communities on arable fields and to compare them with similar phytosociological units from primary habitats, ii) to assess species composition and size of the seedbank, and iii) its relation to above-ground vegetation, water regime and management.

6. 3 Material and methods

Study area

All arable fields under study were situated in the Hessian portion of the Holocene floodplain of the River Rhine about 30 km south-west of Frankfurt, Germany (8°24’08’’ E to 8°26’20’’E and 49°50’20’’N to 49°52’02’’N; 83.9 m to 85.1 m a.s.l.) east of the main channel. Across the whole area, calcareous and extremely fine-grained alluvial soils topping sandy sediments of the Rhine, are predominant (Böger 1991). The climate of the region is relatively warm and dry, with a long growing season (> 250 days with mean temperature > 5°C), a high mean temperature of 10.3 °C and a low mean annual precipitation of 580 mm (Müller-Westermeier 1990). These climatic and hydrological conditions result in a highly variable soil water potential: while winter, spring and early summer may bring floods, the summer period is notably dry. Additionally, due to the high clay content (> 60%) plant-available water is rapidly declining shortly after the retreat of water.

Until the 1950s (Knapp 1954) and even 1960s this area was dominated by species-rich alluvial grasslands extensively managed as hay-meadows. With the start of intensified drainage in the 1920s, structural changes in agriculture and a series of dry years during the 1970s and early 1980s, the arable use was increasingly extended even to the lowest parts of the area (Böger 1991). Especially these depressions are prone to the effects of indirect flooding through a rising ground-water table in the hybrid and fossil floodplain (up to 1 m). Along with the strong seasonal and inter-annual fluctuations of the water level of the River Rhine goes a maximum amplitude of the ground-water table of more than 6 m (Dister 1980; Böger 1991). The closer the sites are situated to the main channel the faster the ground water table rises or falls in accordance to the water regime of the Rhine, while distant sites are characterised by a more stable water regime (Figure 1). As a consequence, areas at the same elevation will be subject to longer periods of inundation close to the river channel than further

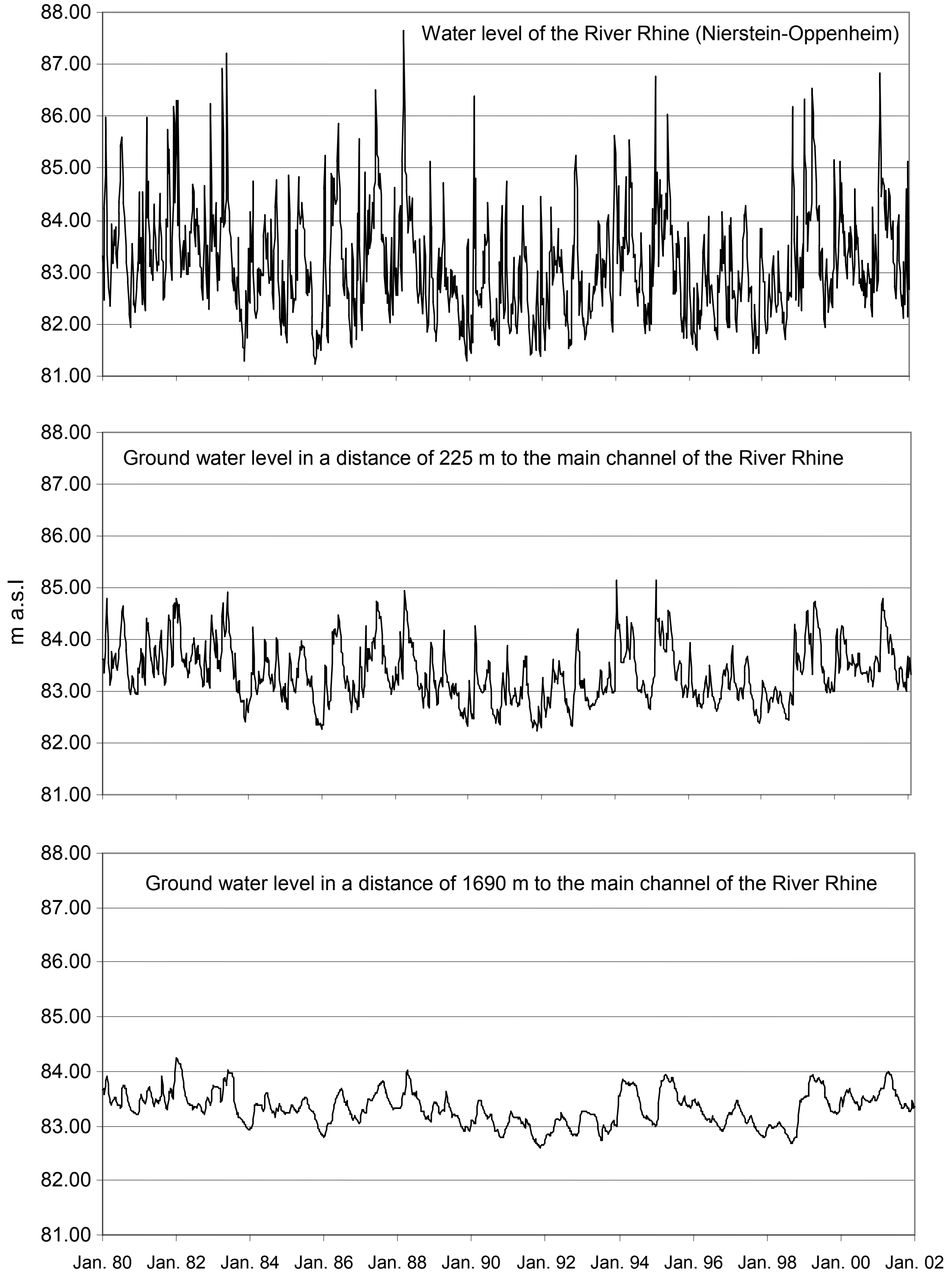

Figure 1. Trend of the water level of the River Rhine and the groundwater level in two different distances to the main channel of the Rhine in the period 1980 to 2001.

away (Table 1). High water levels from March until June are crucial for the successful reproduction of mudflat species, since flooding during winter and early spring with a drawdown before March will give farmers the option to re-plough and re-seed the mudflat habitats. In the period between 1980 and 2000 water regimes facilitating the development of ephemeral wetland vegetation occurred six times (on average every 3.5 years) with at most seven years in between. In 2001 the duration of inundation on sites close to the main channel of the river lasted at least two times as long and at distant sites up to five times as long compared to the period 1980 to 2000 (Table 1).

Table 1. Average time (weeks per year) in the period 1980 to 2000 and number of weeks in 2001 during which the ground water table was raised between March and June above different ground levels (m a.s.l.) at a sites close (C; 225 m) and distant (D; 1690 m) to the main channel of the river Rhine.

	1980 - 2000 yr.$^{-1}$		2001	
m a.s.l.	C	D	C	D
83.9	8.2	1.6	14	8
84.2	4.6	0.1	10	0
84.5	1.6	0	5	0
84.8	0.2	0	0	0
85.1	0.1	0	0	0

Above-ground vegetation

We sampled the composition of vascular plant species in 32 plots of 25 m^2 (5 x 5 m) in June 2001. These relevés constituted an almost complete collection of ephemeral wetland vegetation of secondary habitats in the area, only some sites which were already re-ploughed by the time of the study could not be recorded. At all sites under study, the seeded crops had died back and were subsequently replaced by ephemeral wetland vegetation. Species abundance was estimated on a modified Braun-Blanquet-scale (van der Maarel 1979). Nomenclature of plant species follows Wisskirchen & Haeupler (1998).

Additionally, we compared the floristic composition of mudflat vegetation in arable fields of the present study, with phytosociological data from primary and secondary habitats along the northern Upper Rhine. We used vegetation relevés from temporary flooded arable fields by Oesau & Froebe (1972) and compared these with relevés of primary habitats (Oesau 1972; Dister 1980; Oberdorfer 1992). Phytosociological classification of the species follows Oberdorfer (1983, 1992).

Seedbank

At nine sites where above-ground vegetation was sampled, we also took samples of the soil seedbank. Using a soil corer of 3 cm diameter, at each site 20 cores of 10 cm depth were taken at random locations after removing all plant material from the soil surface. The soil samples represent 141 cm^2 of the soil surface and 1410 cm^3 of the soil volume in each allotment.

We analysed seedbanks with the seedling emergence method over 30 months (Roberts 1981). After removing vegetative plant material the soil samples were transferred to 18 cm x 28 cm Styrofoam trays as a 3 cm thick layer and exposed in free air conditions. The trays 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. Germinating seedlings were identified and removed once every week. Unidentifiable specimens were transferred to pots and grown until they could be named. When germination declined the samples were, after removal of emerging seedlings, regularly crumbled and mixed. To acquire both, the extent of the seedbank of common agrestal species, regularly occurring at terrestrial sites, and the seedbank of the typical ephemeral wetland vegetation, we exposed the samples to different water regimes. For the first 18 month the samples were exposed to terrestrial conditions with no flooding but regular watering to keep them moist. In accordance to findings by several authors (e.g., Ter Heerdt et al. 1999; Moravcová et al. 2001) who stress the importance of stratification under amphibious conditions for the emergence of ephemeral wetland species, prior to the third season of the analysis the samples were first shallowly flooded for three months (January to March) and subsequently kept under waterlogged conditions.

Data analysis

From the vegetation relevés, we derived cover-weighted means of the Ellenberg values for moisture (Ellenberg et al. 1991). Topography of the respective sites and weekly data from the nearest ground water gauge were used to calculate flooding duration for the years between 1980 and 2000 and for 2001, the year of sampling.

Detrended Correspondence Analysis (DCA) was used to explore gradients in the floristic composition of vegetation samples. To reduce their unduly influence on ordination results, rare species (i.e. occurrence in less than 20% of the samples) were down weighted (McCune & Mefford 2002). Prior to analysis the values of species abundance were transferred to a fully numerical 1-9 scale (van der Maarel 1979). Correlations between measures of water regime at the sample sites and the DCA sample scores were analysed with Pearson correlation as suggested by McCune & Mefford (2002).

The Mantel test (Legendre & Legendre 1998) was used to evaluate the similarity between the seedbank and the established vegetation as well as to test for spatial proximity in the vegetation and the seedbank. In the latter case we used analogous to the distance measure in space, the Euclidean distance measure to create the seedbank and vegetation matrices, but comparing seedbank and vegetation composition we used the Sørensen index. To test for the significance of the results we used the randomisation method (3000 runs; McCune & Grace

2002). Prior to the Mantel test the estimated species coverage was replaced by the percentage of the respective class of the Braun-Blanquet scale (van der Maarel 1979).

Effects of the flooding treatment on seedling emergence were tested with the non-parametric Mann-Whitney U-test. Correlations between seedbank density and elevation, as a measure of the overall prevailing water regime, were analysed using the Spearman rank correlation.

For correlations and other basic statistical analyses we used the software package STATISTICA 6.0 (Anon. 2002b). DCA, Mantel test and the related statistical verifications were done with PC-Ord 4.14 (McCune & Mefford 1999).

6. 4 Results

Above-ground vegetation

The DCA ordination had a total inertia of 1.95. The gradient length of axis 1 and 2 both exceeded two standard deviation units: 2.29 and 2.01, respectively. The first axis had the eigenvalue 0.25, while the eigenvalues of axis 2 and 3 were lower (0.16 and 0.12). The DCA ordination graph (Figure 2) showed a separation of the plots according to the crops, which were originally cultivated at the respective sites. While sites with winter cereals are predominately positioned in the lower right corner, sites with rape, mustard and fallow land were situated in the upper left corner. The Pearson correlation coefficient between sample scores and direct as well as indirect parameters of the prevailing water regime showed clear trends along the axes 1 and 2 (Table 2). The Mantel test indicated a weak, albeit not significant, resemblance between the distance of the sites in space and the distance in vegetation composition of all samples ($r_{Mantel} = 0.14$, $P = 0.095$).

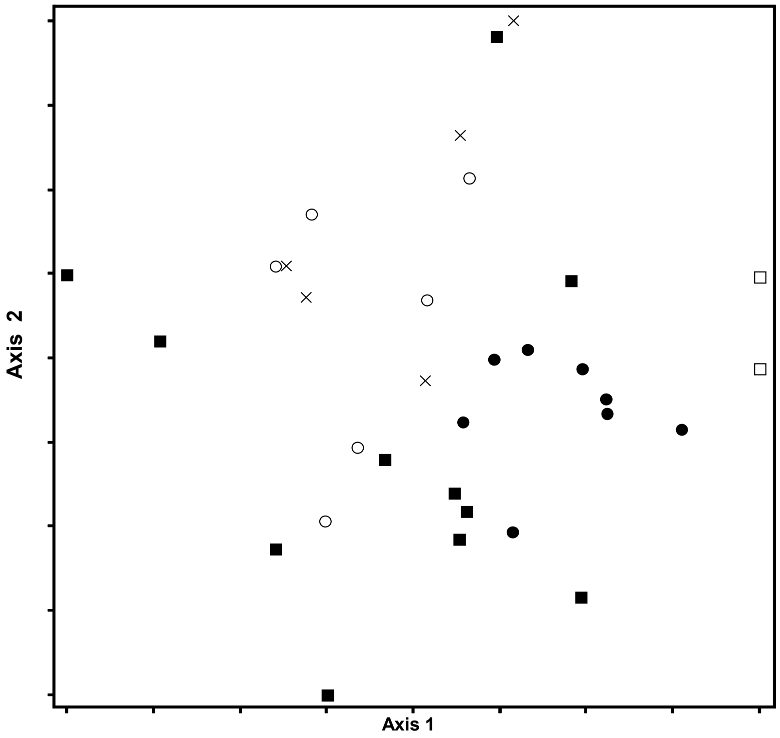

Figure 2. DCA ordination diagram with scores of all relevés plotted along axes 1 and 2. Different symbols represent different crops cultivated on the arable fields under study: Winter crops are represented by filled symbols, i.e. circles in the case of winter barley and squares in the case of winter wheat. Rape and mustard are represented by empty circles and squares, respectively. Fallow land is represented by crosses.

Table 2. Pearson correlation between sample scores on the first two DCA axes and site parameters (N = 32).

	Axis 1	Axis 2
Moisture value	-0.32	-0.34
Elevation	0.45	-0.22
Weeks of inundation (1980-2001)	-0.47	-0.31

Table 3. Plot frequencies (%) of mudflat species in primary and secondary habitats in the northern Upper Rhine region based on four surveys: 1 = Oesau 1972 (in Oberdorfer 1992), 2 = Dister 1980, 3 = Oesau & Froebe 1972, 4 = present study; (M) = mosses; n.m. = not mentioned. Phytosociological classification follows Oberdorfer (1983, 1992).

	Primary habitats		**Secondary habitats**	
	1	**2**	**3**	**4**
Total number of relevés	214	9	17	32
Mean number of species	n.m.	11	13	14
Min number of species	n.m.	6	5	7
Max number of species	n.m.	20	19	26
Isoëto-Nanojuncetea				
Limosella aquatica	100	78	12	6
Cyperus fuscus	23	33	100	22
Gnaphalium uliginosum	64	78	.	3
Riccia cavernosa (M)	72	.	.	.
Physcomitrella patens (M)	59	.	.	.
Botrydium granulatum (M)	60	.	.	.
Centaurium pulchellum	.	.	24	6
Juncus bufonius	.	.	35	94
Lythrum hyssopifolia	.	.	24	.
Bidentetea				
Chenopodium rubrum	37	22	.	.
Ranunculus sceleratus	58	89	12	66
Persicaria lapathifolia	.	22	47	100
Rorippa palustris	.	56	18	22
Atriplex hastata	.	11	12	19
Rumex maritimus	.	22	.	3
Alopecurus aequalis	.	67	.	.
Rumex palustris	.	11	.	.
Persicaria minus	.	11	.	.
Potentilla supina	.	.	24	.
Bidens tripartita	.	.	12	.
Phragmitetea				
Rorippa amphibia	31	100	.	.
Oenanthe aquatica	1	44	.	3
Carex gracilis	.	44	.	.
Phalaris arundinacea	.	11	.	3
Schoenoplectus lacustris	.	11	.	.
Iris pseudacorus	.	11	.	.
Alisma plantago-aquatica	.	.	41	6
Alisma lanceolatum	.	.	24	19
Typha latifolia	.	.	35	3
Phragmites communis	.	.	18	.
Veronica anagallis-aquatica	.	.	12	.
Agrostietea				
Rorippa sylvestris	.	.	59	44
Rumex crispus	.	33	.	22
Agrostis stolonifera	.	.	18	13
Potentilla reptans	.	.	12	.
Stellarietea				
Euphorbia platyphyllos	.	.	35	.
Sonchus arvensis	.	.	12	.
Persicaria aviculare	.	.	47	81
Sonchus asper	.	.	24	44
Persicaria maculosa	.	.	41	22
Chenopodium polyspermum	.	.	12	38
Kickxia elatine	.	.	29	6
Stellaria media	.	.	12	3
Chenopodium album agg.	.	.	12	3
Echinochloa crus-galli	.	.	.	34
Alopecurus myosuroides	.	.	.	25
Anagallis arvensis	.	.	.	22
Atriplex patula	.	.	.	19
Tripleurospermum perforatum	.	.	.	13
Additional taxa				
Veronica peregrina	80	78		
Nymphoides peltata	10	11		
Populus nigra	.	22		
Veronica catenata	53	100	71	94
Salix alba	7	22	24	9
Plantago major agg.	.	22*	41	84*
Juncus articulatus	.	11	76	72
Persicaria amphibia		22	12	16
Epilobium tetragonum	.	.	35	53
Cirsium arvense	.	.	29	28
Lythrum salicaria	.	.	35	3
Poa trivialis	.	.	41	.
Stachys palustris	.	.	35	.
Samolus valerandi	.	.	24	.
Triticum aestivum	.	.	.	38
Epilobium hirsutum	.	.	.	22
Equisetum palustre	.	.	.	16
Agropyron repens	.	.	6	13
Brassica napus	.	.	.	13
Coronopus squamatus	.	.	.	13
Taraxacum officinale agg.	.	.	.	13
Mentha arvensis	.	.	12	.
Myosoton aquaticum	.	.	12	.

* *Plantago major* ssp. *intermedia*

Additional taxa: *Chenopodium hybridum* (rel. 3:6, 4:6); *Poa annua* (3:6, 4:3); *Ranunculus repens* (3:6, 4;3); *Potentilla anserina* (3:6); *Phalaris canariensis* (3:6); P*ortulaca oleracea* (3:6); *Chaenorrhinum minus* (3:6); *Senecio vulgaris* (3:6); *Avena fatua* (3:6); *Valerianella carinata* (3:6); *Apium nodiflorum* (3: 6); *Chenopodium ficifolium* (3:6); *Matricaria inodora* (3:6); *Sparganium ramosum* (3:6); *Scirpus maritimus* (3:6); *Symphytum officinale* (3:6); *Amaranthus retroflexus* (4:9); *Tussilago farfara* (4:9); *Apera spica-venti* (4:6); *Juncus compressus* (4:6); *Bolboschoenus maritimus* (4:6); *Capsella bursa-pastoris* (4:6); *Fallopia convolvulus* (4:6); *Fumaria officinalis* (4:6); *Kickxia spuria* (4:6); *Schoenoplectus tabernaemontani* (4:6); *Solanum nigrum* (4:6); *Sonchus oleraceus* (4:6); *Trifolium repens* (4:6)*; Veronica arvensis* (4:6); etc.

Comparison of floristic composition with similar vegetation studies

The comparison between vegetation relevés of ephemeral wetland vegetation in primary and secondary habitats on arable fields along the northern Upper Rhine indicated some differences in species composition (Table 3). While characteristic species of the class Isoëto-Nanojuncetea like *Limosella aquatica* or *Gnaphalium uliginosum* showed high plot frequencies in primary habitats, these species were much rarer or absent in secondary habitats.

Cyperus fuscus was found in primary as well as in secondary habitats and showed the highest plot frequency in the community described by Oesau & Froebe (1972), which was located in arable fields on the opposite side of the River Rhine. Some species of the class Bidentetea such as *Ranunculus sceleratus* and *Rorippa palustris* occurred in both, primary habitats and in the arable fields under study. Additionally individual species of the class Phragmitetea were more often found in primary habitats (e.g., *Rorippa amphibia*) while others were clearly associated with secondary habitats (e.g., *Alisma lanceolatum*). Most characteristic to the arable field sites was the occurrence of species of the class Agrostietea (*Rorippa sylvestris*, *Agrostis stolonifera*) and a large number of arable weeds such as *Sonchus asper*, *Chenopodium polyspermum* or *Kickxia elatine*, which were completely absent in primary mudflat habitats. This also led to slightly higher species-richness per plot in the secondary habitats.

Seedbank

Altogether 28,724 seedlings emerged from the nine samples. The lowest calculated number of seedlings per square meter was 5,022, while the highest total seed density was 761,961 seeds/m². On average we found 225,756 seeds/m^2 in the upper 10 cm of the soil. In five samples we found more than 100,000 seeds/m^2 of which three contained even more than 300,000 seeds/m^2. A total of 47 different plant species could be identified in the seedbank samples, with an average of 15.7 (11-23) different species per sample. *Juncus bufonius* was by far the most prominent species with the highest maximum seed density (Table 4). While the soil seedbank was dominated by short-lived species typical of agricultural, ruderal or ephemeral wetland habitats, long-lived species typical of low-lying flood meadows (e.g., *Juncus inflexus*, *J. compressus*, *Pseudolysimachion longifolium*) made up only a very small portion.

The total number of seedlings in all samples emerging before and after experimental flooding did not differ significantly. However, when the group of ephemeral wetland species (N = 12) and the group of typical agricultural species (N = 35) were tested separately, only in the former a significant increase in seedling emergence was revealed (Mann-Whitney U-test, $P < 0.001$). In most species flooding of the samples caused a high number of additionally emerging seedlings (Table 4). Of the total 47 species, 23 did only emerge before and 10 only after flooding whereas 14 species were found during both phases. The correlation between the elevation as a measure for the moisture regime prevailing at the sites and the densities in the seedbank was significant ($r = -0.72$, $P \leq 0.05$).

The Mantel test indicated a weak, albeit not significant, resemblance between the spatial proximity of the sites and the seedbank composition ($r_{Mantel} = 0.23$, $P = 0.07$), but revealed a significantly positive resemblance between the seedbank and the vegetation composition of all samples ($r_{Mantel} = 0.34$, $P = 0.03$).

Table 4. Characteristic parameters of the 30 most abundant species in the seedbank of ephemeral wetland vegetation in arable fields (N = 9) and reaction of the species to flooding. Significant differences in seedling emergence before and after experimental flooding of the samples are indicated by an asterisk (Mann-Whitney-test; $\alpha \leq 0.05$). min = minimum; max = maximum.

		Percentage of the total seedbank	Seedling density (m^{-2})			Plot-Frequency	Emerged seedlings		
			Min.	Mean	Max.		before	after flooding	after (%)
Juncus bufonius		85.9	1061	193,910	707,072	100	10,008	14,664	59
Ranunculus sceleratus		4.14	71	9337	33,458	89	618	570	48
Veronica catenata	*	2.73	1627	6162	19,099	100	624	160	20
Plantago intermedia	*	1.65	212	3733	12,591	78	438	37	8
Juncus articulatus		1.44	71	3262	6649	100	182	233	56
Chenopodium polyspermum	*	1.01	71	2279	7569	89	284	6	2
Persicaria lapathifolium	*	0.94	141	2114	13,157	89	257	12	4
Rorripa sylvestris		0.77	283	1729	12,025	33	195	25	11
Rorripa palustris		0.35	71	794	3820	56	79	22	22
Persicaria maculosa	*	0.17	71	393	1203	89	48	2	4
Alopecurus myosuroides	*	0.13	141	299	1698	56	38	0	0
Cyperus fuscus		0.1	71	236	920	44	21	9	30
Juncus inflexus		0.1	71	228	1,981	22	28	1	3
Amaranthus retroflexus	*	0.09	71	204	1203	44	26	0	0
Sonchus asper	*	0.07	71	149	495	67	17	2	11
Echinochloa crus-galli		0.05	0	102	920	11	13	0	0
Agrostis stolonifera	*	0.03	71	79	424	56	10	0	0
Persicaria aviculare		0.03	71	79	354	44	9	1	10
Gnaphalium uligonosum		0.03	71	63	495	22	0	8	100
Alisma plantago-aquatica		0.02	0	55	495	11	0	7	100
Sonchus arvensis		0.02	0	55	495	11	7	0	0
Veronica peregrina		0.02	0	47	424	11	0	6	100
Alisma lanceolata		0.02	71	39	283	22	0	5	100
Juncus compressus		0.02	0	39	354	22	0	5	100
Phacelia tanacetifolia		0.02	0	39	354	11	5	0	0
Veronica arvensis		0.02	141	39	212	11	0	5	100
Anagallis arvensis		0.01	0	31	283	11	4	0	0
Mentha aquatica		0.01	0	31	283	11	4	0	0
Solanum nigrum		0.01	0	31	141	22	4	0	0
Veronica persica		0.01	0	31	283	11	4	0	0

6. 5 Discussion

Above-ground vegetation

Although the gradients found in DCA are relatively short, the grouping of the relevés in ordination space seems to be influenced by the originally seeded crop (Figure 2). Different crops are commonly associated with a characteristic weed flora, with differences most pronounced between winter and summer crops (Cavers & Benoit 1989; Otte 1992). Although flooding may equalise differences of the associated weed flora (Zahlheimer 1979), it seems not to completely blot out differences. Differentiating effects of management may be owing to preparation of the seed bed, time of seeding and differences in the reaction of the crops towards flooding. As in fallow land, on rape fields coverage of the soil in spring is higher than under cereals. The resulting differences in light penetration may be high enough to induce a differentiation in species composition between fields originally sown with rape and cereals.

Beside the effects of the management also the prevailing water regime seems to influence the resulting mudflat vegetation (Table 2). This is in accordance with findings in seedbanks of temporary wetlands in New South Wales, where differences in the time of occurrence, duration and depth of flooding had a high impact on species composition of the above-ground vegetation (Casanova & Brock 2000). Although these effects even can be strong enough to overrule differences in the initial seedbank composition (Seabloom et al. 1998; Nicol et al. 2003) this seems not to be the case in the mudflat vegetation of the present study since the Mantel test revealed a significantly positive correlation between above-ground vegetation and the seedbank composition.

The higher importance of these two factors for the emerging mudflat vegetation is also confirmed by the Mantel test of the individual distances between the sites and above-ground vegetation, which suggests a high spatial variability. This variability is most likely induced by differences in water regime and management, which overrule similar climatic and edaphic conditions in the study area. Our findings are in accordance with other studies that also showed a particularly high spatial and temporal variability of mudflat vegetation in secondary, man-made habitats, such as fishponds (Poschlod et al. 1996; Šumberová et al. in print).

Floristic composition of primary and secondary habitats

The characteristic species of primary habitats, *Limosella aquatica*, is able to germinate immediately after drawdown and is therefore one of the first plants that occur in mudflat communities. But since *L. aquatica* relies on moist soil conditions for germination and establishment (Oesau 1972), it rapidly completes its life cycle during prolonged drawdown and is subsequently replaced by more drought-tolerant species (e.g., *Cyperus fuscus* and *Veronica peregrina*). This suggests that not flooding itself but the period of successive drawdown has a major impact on germination and also on floristic composition of mudflat communities (Casanova & Brock 2000; Nicol et al. 2003; Hölzel & Otte 2004b). In accordance to that, primary and secondary habitats differed also in soil composition; especially the typically high clay content (> 60%) of secondary habitats slows down the descend of the water. This is even amplified through their positioning in isolated depressions without superficial drainage. As supposed by Zahlheimer (1979) some species (e.g., *Lythrum hyssopifolia*) may rely upon these longer time periods with favourable soil moisture conditions and are therefore restricted to secondary habitats. Along the northern Upper Rhine species such as *Juncus bufonius*, *Centaurium pulchellum* or *Samolus valerandi* predominantly occurred in arable fields, which is probably due to the slower retreat of the water at these sites that gives these species a wider time frame for germination, growth and reproduction. In contrast to primary habitats, mudflat communities of secondary habitats contain a higher number of species from related vegetation classes, such as Agrostietea, Phragmitetea or Stellarietea. Many of them (i.e. *Rumex crispus*, *Persicaria aviculare*, *Chenopodium polyspermum*) build up persistent seedbanks and are thus well adapted to the conditions prevailing at the temporary flooded arable fields. Perennials such as *Rorippa sylvestris*, *Ranunculus repens* and *Agrostis stolonifera*, which rely on an extensive root system to re-grow after disturbances are successful in arable land but apparently are not able to tolerate long-lasting submersion related to the regular water regime of primary habitats. Since favourable conditions for germination, growth and reproduction of arable weeds do only occur in secondary habitats these species are lacking in primary habitats of Isoëto-Nanojuncetea communities. The tendency of higher species numbers found in secondary habitats is mostly due to the addition of arable weeds to the usual species pool of mudflats (van der Valk & Davis 1978).

Seedbank composition

Average species numbers in our samples agree with results from other temporal wetland habitats (van der Valk & Davis 1978; Leck & Graveline 1979; Smith & Kadlec 1983). In these studies, seedbanks were also dominated by rather few species while the dominance by a single species like *Juncus bufonius* is quite unusual. However, relatively high densities of *Juncus bufonius* in secondary habitats were also found by Bernhardt (1993). In a review, Leck

(1989) showed that the seedbanks of wetlands are most often dominated by monocots with high longevity.

In the present study most species found in the seedbank were agrestal and mudflat species with high light requirements for germination, strict confinement to open habitats (Baskin & Baskin 2001) and the ability to reproduce within a short period of time. While growth and reproduction of mudflat species in natural habitats is mainly limited by the availability of favourable moisture conditions alone, in secondary habitats agricultural management further limits the development of such species. Usually farmers re-plough the sections of the fields which harbour mudflat species as soon as possible after the descend of the water. Thus in these secondary habitats not only the occurrence of inundation is important but also its duration, which has to last long enough to avoid re-cultivation until the species successfully reproduced.

The main strategies of the mudflat species to cope with this highly variable environment are to build up a persistent seedbank to bridge periods of unfavourable site conditions and to exploit the short time with favourable conditions for growth and reproduction (Bonis et al. 1995). Except for *Alopecurus myosuroides*, all species found in the seedbank are known to build up a long-term persistent seedbank (Grime et al. 1988; Thompson et al. 1997; Hölzel & Otte 2004c). During the irregular and relatively short appearance of mudflat species small-sized seeds are produced and released in large quantities. In temporarily drained ponds, e.g., Poschlod et al. (1996) found that the seed rain of *Alopecurus aequalis* and *Juncus articulatus* may consist of more than 300,000 seeds*m^{-2} and in *Ranunculus sceleratus* a single plant may release up to 56,000 seeds (van der Toorn 1980). Additionally, mudflat species have very short life cycles. *Ranunculus sceleratus* only needs two month after germination until seed set and *Juncus bufonius* flowers within four weeks (Grime et al. 1988). Beyond this, species may react flexible to sub-optimal growing conditions. For example, late emerged individuals of the mudflat species *Chenopodium rubrum* were found to start flowering after a shorter time and at an earlier developmental stages (van der Sman et al. 1993).

Seedbank density

Seed densities in this study are on average much higher than those regularly found in comparable temporary habitats such as glacial marshes (van der Valk & Davis 1978), river marshland (Leck & Graveline 1979), freshwater tidal marshes (Leck & Simpson 1987), wetlands in South Australia (Nicol et al. 2003) or secondary habitats such as regularly drained ponds (Poschlod et al. 1996). Only few maximum densities in wet grasslands in southern

Sweden (Skoglund 1990) and in an Appalachian Sphagnum bog (McGraw 1987) reached values in range with average seed densities found in our study. However, in the latter two studies samples were taken to a soil depth of more than 10 cm. The only two studies we know, in which densities of the diaspore bank were even higher, were conducted in Mediterranean temporary marshes in southern France (Bonis et al. 1995) and along the Guadalquivir in southern Spain (Grillas et al. 1993). But in both cases *Characeae* alone accounted for up to 98% of the total diaspore density. Apart from these habitats with strong natural dynamics, high seed densities are also expected to occur under the conditions of arable management, where seed contents can also reach levels of the above mentioned habitats (Jensen 1969; Cavers & Benoit 1989). In our study seed densities found in agricultural mudflat habitats were much higher than those reported from seedbanks of flood meadows in the same area (Hölzel & Otte 2001). In accordance with this study we found an increase in seed densities in the soil with increasing flooding duration that was also reported by other authors (c.f. Chippendale & Milton 1934; Thompson & Grime 1979). This general increase of seed densities may be seen as an adaptation to irregular and unpredictable disturbances that favour species following a ruderal strategy (Grime 2002).

A comparison of the obtained seed densities of individual species with data from the database by Thompson et al. (1997) showed that most seed densities are in the range of previous analyses, but in case of the three most abundant species i.e. *Juncus bufonius*, *Ranunculus sceleratus* and *Veronica catenata* the values distinctly exceeded the highest mean and maximum numbers found so far. Especially, the maximum seed density of 707,072 seeds*m^{-2} for *Juncus bufonius* not only marks a new record for this species, but to our knowledge is, up to date, the highest seed density found in any higher plant (c.f. Thompson et al. 1997).

Influence of flooding

Among species that showed lower or no additional emergence of seedlings after flooding all but one (i.e. *Veronica catenata*) belong to the group of typical agrestal species in the region. While this can in part be attributed to adverse conditions for germination (i.e. too wet, low oxygen levels; Baskin & Baskin 2001) another reason may be that in seedbank analyses most seedlings regularly emerge within the first year (Ter Heerdt et al. 1996; Thompson et al. 1997). Although this phenomena may be responsible for the higher number of species occurring before flooding than afterwards (23 vs. 10), it is quite astonishing that about 55% of all seedlings emerged after the flooding treatment despite the shorter time period under waterlogged conditions. Most obvious is the positive effect of this treatment in the germination of typical mudflat species such as *Gnaphalium uliginosum* and *Veronica peregrina* as well as the helophytes *Alisma lanceolata* and *A. plantago-aquatica*, in which all individuals emerged after the application of the flooding treatment. Findings by Moravcová et al. (2001) also highlight the importance of cold stratification and flooding for the germination of *Alisma lanceolata*, *A. plantago-aquatica* and *A. gramineum*.

These findings are in accordance to authors who stress the importance of an adequate treatment when assessing the soil seedbank in habitats known to harbour species groups with divergent requirements for germination (van der Valk & Davis 1978; Leck & Graveline 1979; Smith & Kadlec 1983; Gerritsen & Greening 1989). In our study the sequential application of different moisture treatments was found to be particularly useful and led to an increase of detected seeds of typical mudflat species.

Conclusions

Our results highlight the importance of irregularly flooded arable fields as a habitat for ephemeral wetland plant species and communities, which are partly considered as endangered (e.g. *Samolus valerandi*, *Centaurium pulchellum*, *Coronopus squamatus*; Korneck et al. 1996). Since in these strongly disturbed dynamic habitats, seedbanks are of major importance for the long-term preservation of such plant communities, measurements for their preservation have to aim at the maintenance and renewal of the seedbank. In contrast to mudflat plants in primary habitats, which are able to grow and reproduce also in years with only slight drawdown at exposed edges of oxbows and river banks, in secondary habitats successful reproduction and thus replenishment of the soil seedbank is restricted to years with extremely long lasting floods of the Rhine. Thus, reproduction is not only a priori less frequent than in primary habitats, but additionally at risk by human activities. Although in arable weeds generally adverse effects of fertilization and herbicide application are known (Roberts & Neilson 1981; Cavers & Benoit 1989; Otte 1992), the high seed densities and species numbers we found, suggest that the maintenance of the seedbank is not negatively influenced by intensive arable use.

Since farmers want to reduce the losses in crops caused by inundation fields they try to lower flooding frequency and duration by improved drainage or by landfill depressions with soil, which means a complete destruction of the habitat for wetland ephemerals (Täuber & Petersen 2000). After flooding and subsequent emergence of mudflat species from the seedbank it is essential that plants can successfully reproduce. Therefore, it is important to extent the period until the field is re-ploughed after the retreat of flooding water. In fact, even from the farmers' point of view there is no need to re-plough as soon as possible with the aim to reduce seed input. Since the emergence of mudflat species is confined to a relatively short period directly after flooding they are not a real problem for arable crop production anyway. Actually, the described secondary mudflat communities strictly depend on arable use. Without regular disturbances by ploughing the floodplain levels these communities occupy in arable fields would be rapidly colonised by competitive perennial species. Thus, the preservation of these secondary mudflat communities crucially depends on a continuation of arable use at relatively low elevations in floodplains.

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7 The influence of competition by sown grass, disturbance and litter on seedling emergence, early survivorship and final establishment in flood-meadow restoration

Tobias W. Donath, Norbert Hölzel & Annette Otte

Manuscript

7. 1 Abstract

In the beginning of restoration projects aiming at the re-creation of species-rich grassland there is always the question of appropriate measures on restoration sites before the introduction of rare species. In this context the effects of disturbance, litter and simultaneously sown grasses on seedling recruitment are of high interest. Especially sowing of grasses is of high practical relevance since it has the potential of accelerating the incorporation of the newly created meadows into local farming systems.

We studied the effects of simultaneously sown grasses on seedling emergence and recruitment success of six typical flood meadow species in two former arable fields, which were situated in the functional and fossil floodplain along the northern Upper Rhine. Additionally, we set up an experiment in the functional flood-plain to assess the effects of litter and disturbance in an existing grassland.

In most species positive effects of disturbance and negative effects through the application of litter on emergence, survival and establishment went in line with our expectations. The simultaneous sowing of grass revealed no general effect but at the species level in most cases there was a tendency of higher rates of survival and establishment when species grew among sown grass, which may be a result of facilitative effects during the dry summer of 2003.

Much clearer than the treatment effects was the influence of differences in site conditions. While seedling emergence was the same in the fossil and functional floodplain, survival and establishment rates were both significantly higher in the fossil floodplain with its higher and more stable ground-water table.

Our results clearly show that under almost all treatments the introduced species were able to establish successfully stressing the importance of seed limitation for certain vegetation patterns also in regularly flooded meadows. The simultaneous addition of grass did not hamper seedling recruitment, thus implying that this is a feasible measure to advance the incorporation of newly created meadows into farming systems and consequently ensuring the maintenance of these meadows.

7. 2 Introduction

Limited seed dispersal was found to be a major constraint in the restoration of former species-rich plant communities. Consequently, much recent research in the course of restoration measures is focused on active seed introduction of target species. Seeds applied are either obtained from commercial wildflower seed producers (Bullock et al. 2001; Jones & Hayes 1999) or by transferring autochthonous diaspores with plant material (Hölzel & Otte 2003; Jones et al. 1995).

However, even after bridging dispersal limitation by sowing, many species exhibit specific requirements for regeneration niches (Grubb 1977) that may considerably differ from those of adult plants. In this phase coexistent vegetation can have quite diametrical impacts: while under harsh site conditions, i.e. high temperature and low soil water content, facilitation seems to be more important (Greenlee & Callaway 1996; Martinez 2003) under more favourable conditions inhibition through competition for light and water often outweighs these positive effects (Foster & Gross 1998; Lepš 1999). The latter process prevails in relatively productive grasslands, e.g., flood meadows, where disturbance that weakens competitors and create gaps are an essential prerequisite for changes in species composition by introduced seeds to occur (Bullock et al. 1995; Edwards & Crawley 1999).

In contrast to these general assumptions, in the of course grassland restoration on arable fields an acceleration of the development towards a closed sward may be desired. This is to speed up the incorporation of restored sites into agricultural management regimes, beyond high public compensation payments. While the presence of an already closed sward was found to be a major burden for the successful establishment of less competitive herbaceous species (Foster & Gross 1998; Lepš 1999; Tilman 1993), the impact of simultaneously sown grass is less clear (c.f. Bosshard 1999).

In three field experiments we analysed the main effects of sown grass on i) seedling emergence, ii) survival and iii) establishment of six herbaceous grassland species under contrasting hydrological regimes (functional vs. fossil floodplain). Additionally, we assessed the effects of litter application and disturbance on the same traits in an alluvial meadow. To draw conclusions about the effects of the treatments beyond the phase of emergence we followed the fate of the introduced seeds over a period of two years.

The main objectives of the three experiments were:

- To which degree does the application of litter, disturbance and sown grass have an impact on i) seedling emergence, ii) survival and iii) establishment during the first two years of growth?
- Is species enrichment in arable fields hampered by the simultaneous addition of grass seeds and are these effects consistent under two different hydrological regimes?

7. 3 Material and Methods

Study area

The study area is situated in the Hessian portion of the Holocene flood plain of the River Rhine about 30 km south-west of Frankfurt, Germany. The area represents one of the last and most important strongholds of many rare and endangered alluvial grassland species (c.f. Donath et al. 2003).

A winter dyke divides the area into two hydrological compartments. In the fossil flood-plain, landwards the dyke, direct flooding by river water is precluded, but large areas in depressions are submerged by clear ascending ground-water during floods of the river. In contrast, the functional flood plain riverwards of the dyke is exposed to direct flooding by river water of up to 3 m and is closely connected to the water-regime of the Rhine. Due to the prevailing alluvial soils, which are typically of calcareous, extremely fine grained composition (clay content >60 %) and consequently do not only prevent a fast ascend of ground-water during floods but also prevent a fast drainage, the water regime in the fossil-floodplain is in general much more stable than in the functional-floodplain (c.f. Bissels et al. in print). The climatic conditions in the region are relatively warm and dry, i.e. mean temperature of 10.3 °C, mean annual precipitation of 580 mm (Müller-Westermeier 1990), and result in conjunction with the hydrological and edaphic conditions in a highly variable soil water potential.

Study species

The species included in this study (i.e. *Arabis nemorensis*, *Iris spuria*, *Pseudolysimachion longifolium*, *Serratula tinctoria*, *Silaum silaus*, *Viola pumila*; nomenclature according to Wisskirchen & Haeupler 1998; Table 1) are typical of flood meadows along the northern Upper Rhine, but due to dispersal limitation their occurrence is restricted to remnant stands along ditches, paths and in old meadows (Donath et al. 2003). Despite these distribution patterns they are not restricted to meadows of low productivity, but are able to form vital populations also in high yielding grassland (Donath et al. 2004). However, in high productive grassland they depend on a traditional management with mostly only one harvest per year in mid-June, which leaves enough time for the species to re-flower and produce seeds until the end of the vegetation period. Except for *Silaum silaus*, all species are rated as threatened by extinction in the Red List of Germany (Jedicke 1997). *Arabis nemorensis*, *Iris spuria* and *Viola pumila* are even considered as threatened at the Central European scale (Schnittler & Günther 1999). None of the species did occur in the above- ground vegetation, the seed bank at the study sites or in their close surroundings, although they are capable of forming viable populations in such situations (Bissels et al. 2004b and unpublished data).

Table 1. Study species. Listed are the seed mass (SM according to Hölzel & Otte 2004b), the emergence rate under optimal conditions (OC) for germination in a common garden and the Red list status of vascular plants in Germany (RL according to Jedicke 1997).

	RL	OC (%)	SM (mg)
Arabis nemorensis	2	85.8	0.06
Iris spuria	2	72.9	14.62
Serratula tinctoria	3	87.1	1.26
Silaum silaus	--	76.9	2.43
Pseudolysimachion longifolium	3	92.0	0.05
Viola pumila	2	83.9	1.08

Seeds of the species were collected in autumn 2001, subsequently dry stored in darkness at room temperature until sowing on February 5, 2002. This sowing date left enough time for cold stratification in the field, which is ,e.g., crucial for successful germination of *Silaum silaus* (Apiaceae; Baskin & Baskin 2001; Hölzel & Otte 2004c).

Experimental design

We carried out seed addition experiments at three sites. Two of these sites were situated on arable fields in the fossil (FOS) and functional floodplain (FUN), respectively. The third site was situated in an old but still species poor alluvial meadow in the functional floodplain (FUN G).

At the ex-arable fields we tested the effects of sown grass on seedling emergence, survival and establishment using a split-plot design with four blocks. Each block contained three main plots (each 2.30 m x 2.30 m). One was left to natural recruitment and two were sown with 3 and 15 g*m^{-2}, respectively, of a species-poor grass mixture (i. e. *Arrhenatherum elatius*, *Alopecurus pratensis*, *Dactylis glomerata*, *Festuca pratensis*, *Poa pratensis*, *Festuca rubra*). This mixture is regularly used by farmers and conservationists for the recreation of grassland in the region. The seed-densities of 3 and 15 g*m^{-2} represent densities used by farmers for grassland creation and the amount of grass seeds used by landscapers, respectively (Opitz v. Boberfeld 1994; Schlüter 1996).

In the third experiment (FUN G) besides the assessment of the effect of a closed sward, the impact of litter application and disturbance on emergence and early establishment was analysed in a split-split-plot design with four blocks (9.2 m x 2.3 m), where the vegetation in each half of a block (main plot) was disturbed with a rotovator. Within each main plot only one half (subplot) was covered with a 2 cm thick layer of hay. This plant material originated from a species-poor grassland dominated by graminoid species that also lacks the study species. This thickness of litter was chosen since it represents the usual amount of plant material applied in restoration projects with the scope of re-establishing species-rich flood meadows by diaspore transfer with plant material (Hölzel & Otte 2003).

In February 2002 one hundred seeds of each species were sown separately into the 6 sub-plots and sub-sub-plots (0.3 x 0.3 m), which were placed within each of the main plots (FUN/FOS) and subplots (FUN G), respectively. In the grassland the litter was applied immediately after the sowing of the study species took place.

At all sites the number of emerged seedlings and the total number of individuals of the six species was monitored three times a year during the main vegetation period (late May, late July and late September) in 2002 and 2003. At each count new seedlings were marked with differently coloured sticks to follow their individual fate. As a measure for the treatment effects on the vegetation at the experimental sites, cover of sown grass and litter as well as open soil were visually estimated at the main plot level in the arable fields and the meadow, respectively. While in the meadow standing biomass was cut with a cutterbar mower and removed in mid June (traditional mowing date in the region), in the arable field, analogous to maintenance measures, biomass was cut and removed in autumn.

Data analysis

From the data we derived the cumulative seedling emergence rate (*CE*) and survival rate (*SR*) of the seedlings. The cumulative seedling emergence rate was defined as the sum of all newly emerged seedlings up to each counting date. The survival rates of the seedling between two counting dates was calculated as follows: $SR_i = (S_i - N_i)/S_{i-1}$, which is the total number of seedlings (*S*) found at the counting date (*i*) minus the number of newly emerged seedlings at this date (N_i) related to the total number of seedlings found at the previous counting date. Since seedlings were counted six times we could derive five survival rates ($T_{12} - T_{56}$). The overall survival rate (*ST*) is the total number of individuals present after two years (*ET*) in relation to the total number of seedlings that have emerged (*CT*).

To analyse the overall effects of the applied treatments on *SR* and *CE* we carried out a factorial repeated-measures ANOVA with litter, disturbance (FUN G) or grass seed addition (FUN/FOS) as fixed factors and block as a random factor. In the split-split-plot design the effects of disturbance were tested against its interaction with blocks, the effect of litter and its interaction with disturbance against the three-way interaction block-disturbance-litter. The species effect and its interactions were tested against the residual variance among sub-sub-plots. An analogous approach was chosen in the grass seed addition experiments: the grass effect was tested against its interaction with blocks, and the species effects as well as its interactions against the residual variance among the sub-plots. The treatment effects at the species level and in case of the univariate ANOVAs from T_{12} to T_{56} were tested analogously. Due to repeated counting at the same plots over two years for the within subject factors (i.e. counting date) the assumptions of 'circularity' and 'compound symmetry' were not fulfilled (v. Ende 1993) and MANOVA was used to test these factors. For MANOVA results the *P*-values were derived from Pillais-trace (Quinn & Keough 2002). As post-hoc tests we used LSM, which were Tukey-adjusted for multiple comparisons (Anon. 1999b). To assess the differences between the sites FUN and FOS with respect to the cumulative emergence rate (*CT*), the overall survival rate (*ST*) and the total number of established species (*ET*) we applied multiple t-tests. In cases of multiple testing the experiment-wise α was kept at 0.05 by Bonferroni-correction and prior to analyses data was subjected to angular transformation (Zar 1999). All statistical analyses were done using SAS 8.2 (Anon. 1999c).

7. 4 Results

Effects of sown grass

For both sites, FUN and FOS, repeated measurement analyses revealed significant effects of time, species, their interactions and grass*species on the survival rate (Table 2). According to the univariate ANOVA the different species showed almost always significantly different survival rates. Grass seed addition affected the survival rates differently for different species, which was shown by significant species by grass interactions in three instances, whereas the main effect of grass across all species was never significant during the two years. Similar results were found for cumulative emergence from T_{12} to T_{56}: there were only significant results for time, species and their interaction in the repeated measurement analysis but no effect of sown grass and its interactions (results not shown). Although in most cases highest values for the rates of cumulative emergence, survival and establishment at the end of the second year were found when grass seeds were added only in few species significant results were obtained (Table 3). In these cases the effect on survival was not consistent: for *Serratula tinctoria* (in FUN) survival was highest under 15 g*m^{-2} of grass seeds, while in FOS for *Serratula tinctoria* survival was highest under 3 and 15 g*m^{-2} of added grass seeds. Only at site FUN this higher survival in *Serratula tinctoria* led to a higher rate of established individuals.

Table 2. Effects of grass seed addition on the survival rate in arable fields: listed are p-values of the repeated-measures analysis as well as the univariate ANOVA at T_{12} to T_{56}. Significant results are in bold: in case of BS and WS results are significant with an α of 0.05, for the multiple ANOVAS at T2 to T6 the Bonferroni-corrected α of 0.01 is used.

Repeated Measurement			**Univariate ANOVA**				
Site FUN			**T_{12}**	**T_{23}**	**T_{34}**	**T_{45}**	**T_{56}**
BS	**G**	0.72	0.31	0.87	0.06	0.28	0.57
	S	**0.007**	**<0.0001**	**<0.0001**	0.09	**0.004**	**0.0001**
	G*S	**0.04**	0.89	0.77	**0.005**	**0.01**	0.07
WS	**T**	**<0.0001**	--	--	--	--	--
	G*T	0.28	--	--	--	--	--
	S*T	**<0.0001**	--	--	--	--	--
	G*S*T	0.14	--	--	--	--	--
Site FOS							
BS	**G**	0.54	0.73	0.58	0.77	0.54	0.84
	S	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**0.0005**	**0.0002**
	G*S	**0.03**	0.41	**<0.0001**	0.44	0.61	0.67
WS	**T**	**<0.0001**	--	--	--	--	--
	G*T	0.82	--	--	--	--	--
	S*T	**<0.0001**	--	--	--	--	--
	G*S*T	0.92	--	--	--	--	--

G = Grass seed addition; S = Species; T = Time; BS = between-subjects factors; WS = within-subject factor.

Survival rates were significantly higher in the fossil flood-plain than in the functional floodplain (mean ± 95 % confidence interval; 59.8 ± 7.2 % vs. 18.9 ± 5.6 %; *n* = 72; Bonferroni-corrected α = 0.017). Despite higher emergence rates at least in some species in the functional floodplain (e.g., *Arabis nemorensis*, *Serratula tinctoria*, *Viola pumila*) survival rates were across the board higher in the fossil floodplain, e.g., twenty fold in case of *Viola pumila*. Analogously, the number of established individuals after two years was significantly higher in the fossil flood-plain (FOS: 11.3 ± 2.1 % vs. FUN: 2.0 ± 0.6 %). In contrast, seedling emergence did not differ significantly between these two sites (FOS: 17.1 ± 2.3 % vs. FUN: 13.1 ± 2.3 %) and patterns of emergence were also quite similar (Figure 1).

There were also differences between sites with regard to the effect of grass seed addition on the cover of grass (Figure 2). In the first year the cover of grass was on average higher in the fossil floodplain while the opposite was true in the second year. But differences in cover of grass were found to be significant only between 0 and 15 g*m^{-2} in the fossil and functional flood-plain at T2/T3 and T5/T6, respectively.

Table 3. Effects of grass seed addition on the total seedling emergence rate (*GT*), the total survival rate (*ST*) and the total rate of individuals established (*ET*) at the end of the second year at the species level in arable fields. Listed are the mean and the standard error of the mean. Different letters denote significant differences between the three treatment levels as revealed by Tukey adjusted LSM post-hoc significant ANOVA results.

Site FUN	***GT***			***ST***			***ET***		
	0	**3**	**15**	**0**	**3**	**15**	**0**	**3**	**15**
All	13.2 (1.4)	14.8 (1.5)	11.5 (1.5)	17.7 (5.0)	19.6 (5.0)	19.6 (5.2)	1.8 (0.8)	2.3 (1.4)	2.0 (0.5)
AN	6.3 (0.9)	5.3 (1.7)	6.8 (2.5)	0.0 (0.0)	13.8 (13.8)	0.0 (0.0)	0.0 (0.0)	1.3 (1.3)	0.0 (0.0)
IS	10.8 (2.0)	8.3 (2.7)	5.5 (2.4)	51.7 (13.3)	51.1 (13.2)	44.3 (21.2)	6.0 (1.9)	4.8 (2.4)	2.3 (0.9)
SS	14.3 (2.6)	14.8 (3.0)	10.3 (2.8)	10.5 (3.7)	15.6 (7.3)	40.9 (12.6)	1.5 (0.6)	2.8 (1.8)	3.3 (1.1)
ST	24.3 (2.7)	30.8 (4.6)	25.3 (2.9)	**7.9 (5.2)^{ab}**	**3.6 (2.3)^{a}**	**19.0 (2.3)^{b}**	**2.0 (1.4)^{ab}**	**1.3 (0.9)^{a}**	**4.8 (0.6)^{b}**
PL	3.0 (1.5)	5.5 (1.9)	2.3 (0.9)	32.7 (15.4)	22.2 (13.6)	0.0 (0.0)	1.0 (0.4)	1.8 (1.2)	0.0 (0.0)
VP	20.5 (2.4)	23.8 (4.0)	19.3 (5.8)	3.6 (3.6)	11.3 (7.9)	13.3 (3.5)	0.5 (0.5)	1.8 (1.0)	2.0 (0.4)
Site FOS	***GT***			***ST***			***ET***		
	0	**3**	**15**	**0**	**3**	**15**	**0**	**3**	**15**
All	16.6 (2.0)	17.2 (2.1)	17.6 (2.0)	57.9 (5.5)	59.8 (7.3)	61.6 (6.4)	10.6 (1.9)	11.6 (2.1)	11.6 (1.7)
AN	12.5 (4.3)	17.8 (3.4)	7.8 (2.3)	14.1 (12.1)	5.9 (3.4)	4.5 (4.5)	0.5 (0.3)	0.8 (0.5)	0.5 (0.5)
IS	17.3 (7.0)	13.8 (6.5)	15.5 (3.7)	69.4 (9.4)	89.5 (4.4)	72.4 (14.2)	12.8 (6.2)	12.3 (6.0)	10.8 (3.0)
SS	26.0 (2.7)	27.5 (2.5)	28.0 (1.8)	**81.6 (3.5)^{ab}**	**90.7 (3.4)^{a}**	**72.3 (6.5)^{b}**	**21.3 (2.6)^{ab}**	**24.8 (1.7)^{a}**	**20.0 (1.4)^{b}**
ST	20.8 (4.2)	22.5 (1.0)	25.8 (2.8)	**63.4 (3.8)^{a}**	**77.7 (4.2)^{b}**	**77.8 (3.4)^{b}**	13.5 (3.3)	17.5 (1.3)	20.3 (2.9)
PL	4.5 (1.0)	1.5 (1.0)	5.8 (2.3)	47.4 (11.1)	31.3 (18.8)	77.1 (14.2)	2.3 (0.8)	1.0 (0.7)	3.5 (0.6)
VP	18.8 (1.4)	20.3 (2.1)	22.8 (2.5)	71.9 (4.0)	63.9 (6.9)	65.1 (9.7)	13.5 (1.3)	13.3 (2.4)	14.5 (2.3)

FUN = arable field in the functional flood-plain; FOS = arable field in the functional flood-plain; 0, 3, 15 = addition of grass seeds in g*m^{-2}; All = across all species; AN = *Arabis nemorensis*; IS = *Iris spuria*; ST = *Serratula tinctoria*; SS = *Silaum silaus*; PL = *Pseudolysimachion longifolium*, VP = *Viola pumila*.

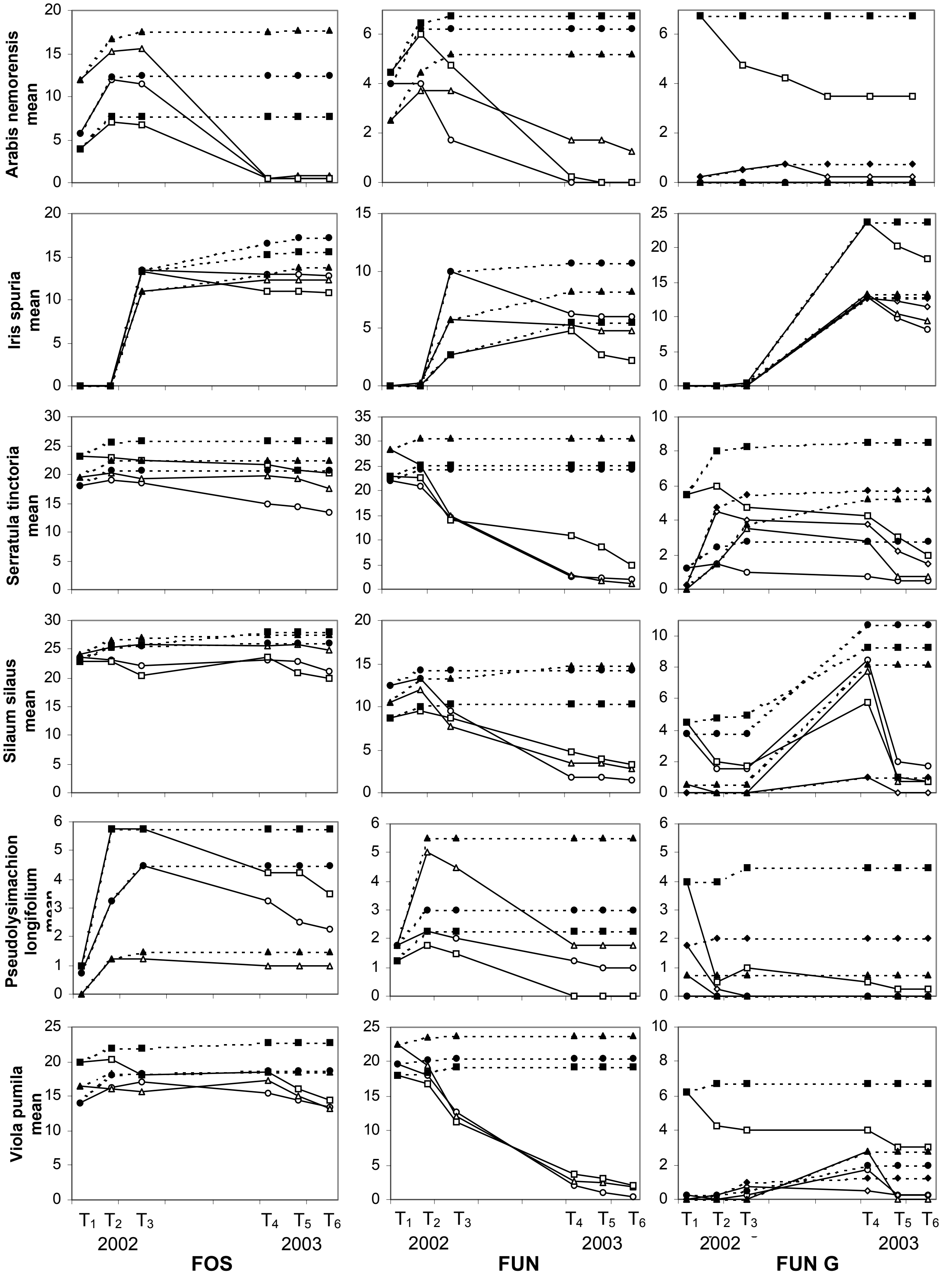
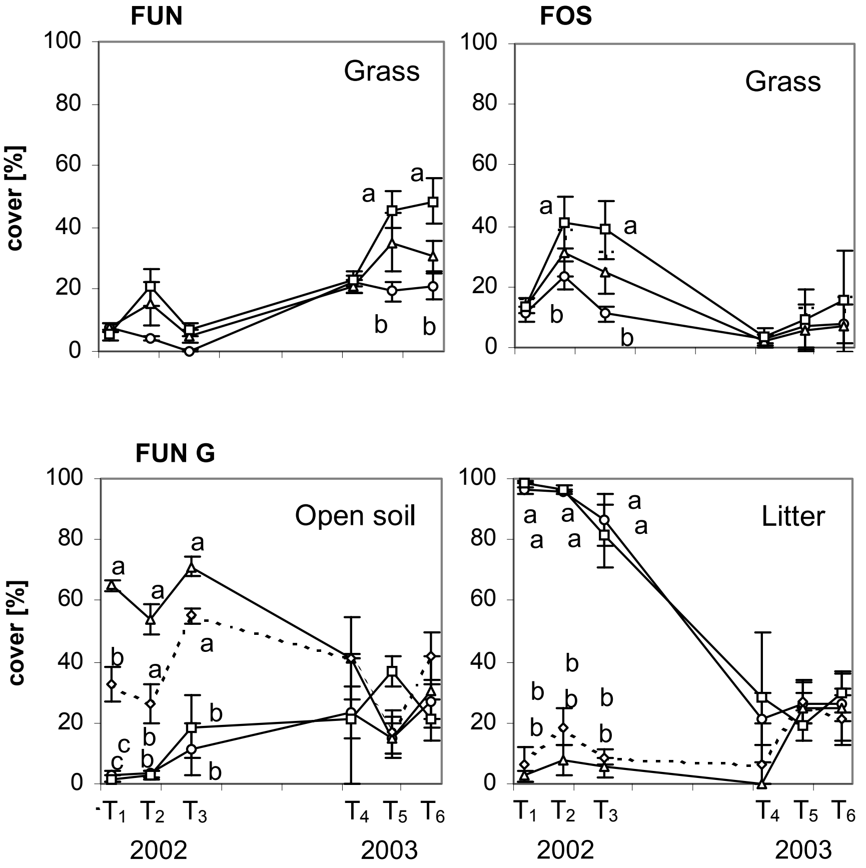


Figure 1. Effects of treatments during the 2 years on cumulative emergence (filled symbols) and seedling establishment (empty symbols) in arable fields in the fossil (FOS) and functional (FUN) floodplain as well as in a grassland in the functional floodplain (FUN G). In the case of FOS and FUN circles represent 0 g*m^{-2}, triangles g*m^{-2} and squares 15 g*m^{-2} of grass seed addition. For FUN G circles represent the treatment D+L+, triangles D-L+, squares D+L- and diamonds D-L- (abbreviations as given in figure 1). Please note that for reasons of clarity the ordinates are differently scaled.



F**igure 2.** Effects of treatments in arable fields in the fossil (FOS) and functional (FUN) floodplain as well as in a grassland in the functional floodplain (FUN G) on cover of grass, respectively, open soil and litter. Shown are the means and their standard error; different letters indicate significant differences as revealed by Tukey adjusted LSM post-hoc significant ANOVA results at each counting date. In the case of FOS and FUN circles represent 0 g m^{-2}, triangles 3 g m^{-2} and squares 15 g m^{-2} of grass seed addition. For FUN G circles represent the treatment D+L+, triangles D+L-, squares D-L+ and diamonds D-L-; D = disturbance (+) vs. no disturbance (–); L = litter added (+) vs. not added (-).

Effects of a closed sward, disturbance and litter

The effects of the treatments as revealed by MANOVA of the within subject effects for the survival rate showed that only time and its interaction with species as well as with disturbance were significant (Table 4). The test of the between subject effects (BS) also revealed a significant interaction of litter with disturbance as well as with species, which all also had a significant main-effect. Univariate ANOVA showed that most of these effects were significant through the whole experiment (i.e. disturbance, litter, species, litter*species) while the interaction disturbance*litter was not significant in the end. The effects of disturbance and litter were significant on the cumulative number of emerged seedlings only during the end of the first year in which most of the seedling emergence occurred, while species and disturbance*litter effects were significant through the whole experiment (results not shown).

Despite significant effects of the treatments on seedling emergence and survival of the species only in *Arabis nemorensis* this difference in emergence rate and survival rate carried forward into the number of established individuals at the end of the second year (Table 5). In all three variables the best performance was observed when the sward was disturbed but no litter applied (D+L-). Only *Silaum silaus* did not follow the general trend of highest emergence and survival under this treatment. This species showed the best survival under the protection of litter (L+), while for *Arabis nemorensis* and *Viola pumila* it was vital to have no litter cover.

Table 4. Effects of disturbance and litter on the survival rate in a flood meadow: listed are p-values of the Repeated-Measures Analysis as well as of the Univariate ANOVA for the time spans T_{12} to T_{56}. Results which are significant are in bold: in case of BS and WS results are significant with an α of 0.05, and for the multiple ANOVA at T_{12} to T_{56} the Bonferoni-corrected α of 0.01 is used.

Repeated Measurement			**Univariate ANOVA**				
Site	**FUN G**		**T_{12}**	**T_{23}**	**T_{34}**	**T_{45}**	**T_{56}**
BS	**D**	**0.0001**	**0.001**	**0.0006**	**0.002**	**0.009**	**0.0004**
	L	**0.0001**	**0.0004**	**0.0009**	**0.0004**	**0.0009**	**0.007**
	D*L	**0.002**	**0.002**	**0.01**	**0.008**	0.02	0.07
	S	**0.002**	**0.0007**	**0.0002**	**0.0002**	**<0.0001**	**<0.0001**
	D*S	0.11	0.02	0.058	0.09	0.05	0.39
	L*S	**0.003**	**0.0007**	**0.01**	0.36	**0.002**	**0.007**
	D*L*S	0.09	0.06	0.0615	0.24	0.04	0.39
WS	**T**	**<0.0001**	--	--	--	--	--
	D*T	**0.04**	--	--	--	--	--
	L*T	0.53	--	--	--	--	--
	S*T	**<0.0001**	--	--	--	--	--
	D*L*T	0.32	--	--	--	--	--
	D*S*T	0.19	--	--	--	--	--
	L*S*T	0.44	--	--	--	--	--
	D*L*S*T	0.25	--	--	--	--	--

D = disturbance; L = Litter; S = Species; T = Time; BS = between-subjects factor; WS = within-subject factor.

As expected, disturbance and the application of litter had significant effects on the proportion of open soil or cover of litter (Figure 2): when no litter was applied (L-) its cover was significantly lower and proportion of open soil higher than in the L+ treatment. While these effects were quite clear during the first year, differences in open soil and litter were much smaller irrespective of the applied treatment in the second year, even with an increasing portion of open soil in the undisturbed plots.

Table 5. Effects of the four treatment combinations of disturbance and litter application in a grassland in the functional floodplain (FUN G) on the total seedling emergence rate (*GT*), the total survival rate (*ST*) and the total number of individuals established (*ET*) at the end of the second year at the species level. Listed are the mean and the standard error of the mean. Different letters denote significant differences between the three treatment levels as revealed by Tukey adjusted LSM post-hoc significant ANOVA results.

FUN G	***GT***				***ST***				***ET***			
	D-L-	**D+L-**	**D-L+**	**D+L+**	**D-L-**	**D+L-**	**D-L+**	**D+L+**	**D- L-**	**D+L-**	**D-L+**	**D+L+**
All	**4.8 (1.5)**^{a}	**9.9 (1.7)**^{b}	**5.0 (1.4)**^{a}	**3.9 (1.1)**^{a}	19.3 (6.0)	35.7 (6.7)	15.1 (6.4)	23.6 (7.7)	1.8 (0.9)	4.7 (1.7)	1.8 (0.9)	2.3 (1.0)
AN	**0.8 (0.8)**^{a}	**6.8 (2.0)**^{b}	**0.0 (0.0)**^{a}	**0.0 (0.0)**^{a}	**8.3 (8.3)**^{a}	**62.1 (12.9)**^{b}	**0.0 (0.0)**^{a}	**0.0 (0.0)**^{a}	**0.3 (0.3)**^{a}	**3.5 (1.0)**^{b}	**0.0 (0.0)**^{a}	**0.0 (0.0)**^{a}
IS	12.8 (2.9)	23.8 (5.9)	13.3 (4.6)	13.0 (6.2)	89.2 (6.6)	73.4 (14.9)	55.8 (20.7)	60.5 (7.7)	11.5 (3.0)	18.5 (7.3)	9.5 (3.2)	8.3 (4.4)
SS	**1.0 (1.0)**^{a}	**9.3 (3.3)**^{ac}	**8.3 (2.6)**^{bc}	**10.8 (2.9)**^{bc}	0.0 (0.0)	5.0 (5.0)	29.5 (23.9)	13.4 (7.8)	0.0 (0.0)	0.8 (0.8)	0.8 (0.5)	1.8 (1.0)
ST	5.8 (2.3)	8.5 (1.7)	5.3 (3.4)	2.8 (1.2)	19.0 (8.7)	26.5 (9.8)	5.4 (5.4)	33.3 (23.6)	1.5 (0.9)	2.0 (0.7)	0.8 (0.8)	0.5 (0.3)
PL	**2.0 (1.7)**^{ab}	**4.5 (0.5)**^{a}	**0.8 (0.8)**^{ab}	**0.0 (0.0)**^{b}	0.0 (0.0)	5.0 (5.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	(0.3) 0.3	0.0 (0.0)	0.0 (0.0)
VP	1.3 (0.9)	6.8 (1.7)	2.8 (2.4)	2.0 (0.9)	25.0 (25.0)	42.2 (11.6)	0.0 (0.0)	8.3 (8.3)	**(0.3) 0.3**^{a}	**3.0 (1.2)**^{b}	**0.0 (0.0)**^{a}	**0.3 (0.3)**^{a}

All = Across all species; AN = *Arabis nemorensis*; IS = *Iris spuria*; ST = *Serratula tinctoria*; SS = *Silaum silaus*; PL = *Pseudolysimachion longifolium*, VP = *Viola pumila*; further abbreviations as given in Figure 2.

7. 5 Discussion

The significant effects of time, species and their interaction goes in line with expectations that seedling emergence changes over time, i.e. in most species the overwhelming number of seedlings was found at the first counting date. The patterns of seedling emergence also differed between species, i.e. hard seeded species such as *Iris spuria* shared later onset of germination (Baskin & Baskin 2001; Hölzel & Otte 2004c). As found in other field experiments, rates of seedling emergence at all experimental sites and across all treatments were lower than in the controls in a common garden, where seeds were watered daily (Kotorová & Lepš 1999). Neither seedling emergence in the common garden nor treatment effects at the experimental sites suggest a reciprocal relationship between rarity, seedling emergence, respectively and establishment. In contrast, *Iris spuria*, the rarest of the study species, was at all experimental sites one of the most successful ones with much higher or at least similar establishment rates as *Silaum silaus*, the least endangered species. The finding that under almost all treatments in the experiments rare and endangered species became established confirms findings that even in regularly inundated flood meadows seed availability and dispersal limitation are crucial factors determining recent vegetation patterns and restoration success (Bissels et al. 2004; Donath et al. 2003).

Effects of sown grass

The non-significant effects of sown grass between counting dates (Table 2) and over the whole experiment (Table 3) on seedling emergence can be seen as a consequence of the simultaneous development of the sown grasses and herbs in the former arable fields. Thus, the effect of initial composition (Egler 1954) where the earlier arrival of one species determines the outcome of competition between these two through, e.g. competition for light (Perry et al. 2003) could not come into effect. By the time the coverage of grass peaked (end of July) and light interception reached levels at which germination is probably lowered (Foster & Gross 1998; Jutila & Grace 2002; Lepš 1999; Williams 1983) most of the emergence of sown herbs had already taken place. Subsequently, competition by a dense root system of surrounding vegetation could lower chances of survival by hampering rooting of seedlings for water and nutrient uptake (Snaydon & Howe 1986). But at this early developmental stage the root system of the sown grass can be expected to be low in analogy to above-ground cover. Consequently, our results suggest that the presence of safe sites, which are essential for successful emergence of seedlings (Grubb 1977) was not significantly narrowed by the sown grass.

In conjunction with the development of grass (Figure 2) it can be seen that the interactive effect between species and grass mainly occurred when coverage of grass prevailed for some time (FOS) or was raised (FUN). At the latter site the significant result on survival at T_{34} despite similar grass coverage between treatment levels may be a result of higher below-ground competition of the root system which was still present from the year before. While this goes in line with the findings of several authors that surrounding vegetation will lower recruitment success (Foster & Gross 1998; Kotorová & Lepš 1999; Lepš 1999) there also seem to occur some, albeit weak, facilitative effects, which led in almost all species to raised rates of survival and establishment when grass seeds were added. Facilitative effects most likely occur under harsh, e.g., dry site conditions (De Jong & Klinkhamer 1988; Holmgren, et al. 1997; Tielbörger & Kadmon 2000). Along the northern Upper Rhine dry periods occur on a regular basis during summer, when low precipitation and high temperatures in combination with soils of high clay content lead to a rapidly decreasing soil water content. Water stress was especially high in 2003 with only 261 mm precipitation from March to October and compared to 530 mm in 2002. During this period also mean temperatures were 1.3 °C higher in 2002 (mean 15.0 °C). Additionally, daily maximum temperatures were elevated by 2.3 °C to 23.0 C. During such periods seedlings are exposed to increased thermal stress and shading by the surrounding vegetation lowers transpiration (Hutchings & Booth 1996b; Larcher 1995), thus already at the first counting date in 2003 an extreme die-off of seedlings was observed in the functional flood-plain. Only in the fossil flood-plain the deficit in precipitation could be compensated by a still higher groundwater table. Consequently, while seedling emergence was hardly different between the two hydrological compartments the lower number of established plants in the functional flood-plain went inline with significant differences in survival rates. Thus, although germination boosted by inundation proved to greatly enhance recruitment success at an experimental restoration site nearby in the fossil flood-plain (Hölzel & Otte 2003) the effects of different hydrological regimes on survival seems to be more decisive for the final number of established individuals than the number of emerged seedlings. In the long run, such differences in water regime through their impact on seedling emergence and survival result in distinct patterns of plant assembly along hydrological gradients in flooded areas (Blom 1999; Casanova & Brock 2000; Leyer 2002).

Role of litter in a closed sward

While only a small effect of the sown grass was found, a significant effect of disturbance in an existing grass sward was obvious. Disturbance of an existing sward is seen as an essential prerequisite for successful recruitment of introduced species in grasslands (Kotorová & Lepš 1999; Lepš 1999) since it lowers both above- and below-ground competition. While a high and closed canopy leads to increased competition for light (Keddy et al. 1997) a developed root system reduces the supply of nutrients and water to a degree were the seedlings are at greater risk of death (Morgan 1997). In addition to lowered competition in the course of floods, also extreme weather events, such as the dry summer in 2003, are capable to open niches for vegetative and generative regeneration. Although this was observed in the non-disturbed plots at the site FUN G, the increase in open soil did not diminish the effect of the disturbance treatment on total survival during the two years as well as it could not overrule the positive effects on total emergence, survival and establishment in the D+L- treatment. The reason for this may be that after droughts, opposite to disturbance by floods, where moist conditions after the retreat of the water may boost germination (Hölzel & Otte 2003), it takes time until water supply recovers to levels supporting successful seedling recruitment. By the time this has happened, there is the risk that competitive species fully recover before germination can take place in addition to induced seed dormancy due to high temperatures (Baskin & Baskin 2001).

The general effects of disturbance alone led in all but one species to higher rates of seedling emergence. Only in *Silaum silaus* the positive effect of disturbance alone was diminished by the application of litter. Additional effects of litter on emergence were shown by Foster & Gross (1997) to positively correlate with productivity at a site. Litter may negatively affect seedling emergence in several ways such as by excluding environmental cues for germination, e.g., light (Williams 1983), chemical compounds dissolved from the litter or it may act as a mechanical barrier (Bosy & Reader 1995; Facelli 1994; Jensen & Meyer 2001). Litter may indirectly lower recruitment success through an increase in herbivorous invertebrates or the seeds' susceptibility to pathogens (Facelli 1994), on the other hand seed predation by rodents may be lowered by a litter layer (Hulme 1994; Reader 1993).

In general, the removal of litter greatly enhances recruitment success in species (Goldberg & Werner 1983; Lepš 1999), but small amounts of litter are capable to prevent seedling desiccation (Fowler 1986; Hamrick & Lee 1987). Species with hard coated seeds, e.g., *Iris spuria*, may positively react towards a litter cover since destructive agents break the physical dormancy more rapidly under a stable moisture regime (Baskin & Baskin 1983). Such an effect probably accounts for the delayed germination and emergence of *Iris spuria* at FUN G where surrounding vegetation presumably lowers moisture levels more than at the arable fields. In case of *Silaum silaus* the positive effect of litter may also be a result of its relatively large seeds. Due to higher reserves, which can be committed in early development large-seeded species are less susceptible towards the impact of litter (Gross 1984; Jensen & Gutekunst 2003) as well as surrounding vegetation (Jakobsson & Eriksson 2000; Turnbull et al. 1999). Consequently, no or even positive effects may occur (Moles & Westoby 2002). While with increasing seed size gap dependence deludes, small seeded species often show distinct reactions towards variation in gaps (Krenová & Lepš 1996). The only species, in which effects of litter and disturbance were significant over all three response variables, was *Arabis nemorensis*. As *Pseudolysimachion longifolium*, this species has extremely small seeds which results in a strong dependence on gaps for successful establishment in closed swards (Grime 2002).

Conclusions

While the study clearly showed that gaps in closed swards facilitate in most cases recruitment success the effects of litter application as well as grass seed addition proved to be quite unpredictable in the present experimental approach. The naturally occurring variation of site conditions had a greater impact especially on survival and establishment success than treatments that mimic restoration measures. As a consequence, theoretical considerations about mechanisms controlling recruitment success may be found to be true under a strongly controlled experimental approach, but prove to be hard to confirm under field conditions, where biological, morphological, edaphical and meteorological constraints vary to a wider extent (Ryser 1993) and treatment effects are additionally blurred by interactive effects (Xiong et al. 2003). The only way to catch these differences in time and space is not only to keep track of the development for several years, but to repeat the same experimental approach for several years in a row.

There seems to be a sensitive balance between the different factors influencing recruitment success, which concurs with theoretical considerations of the non-equilibrium conditions (Huston 1994). High variability of environmental factors in time and space changes the influence of treatment effects, i.e. whether they show facilitative or inhibitory effects (Holmgren et al. 1997). In this context, species can circumvent unfavourable site conditions either by building up a long term persistent seedbank, which in grasslands is done only by a small portion of species (e.g, Hölzel & Otte 2004a), or by vegetative persistence in combination with generative reproduction. In the latter case, also rare events of successful seedling recruitment will be sufficient to maintain a vital population structure (Bissels et al. 2004a).

In the context of grassland restoration projects our results suggest that the establishment of target species is not hampered by simultaneously sown grass in highly variable habitats like flood-plains. This makes it easier to bring together interests of farmers and conservationists. Since through sowing of grass, restored grassland will faster yield quantities and qualities worth harvesting, it accelerates the integration of restored sites into local farming systems, which is urgently needed to maintain the newly created diversity. Subsequently, this will lower costs spend purely for maintenance measures and will improve acceptance of restoration measures by locals.

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8 Perspectives for incorporating biomass from non-intensively managed temperate flood meadows into farming systems

Tobias W. Donath, Norbert Hölzel, Stephanie Bissels & Annette Otte

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8. 1 Abstract

Due to their high value for biodiversity preservation, flood mitigation and nutrient retention, the re-creation of flood-meadows is presently one of the main targets in restoration projects along large Central European lowland rivers. Like other semi-natural grasslands, flood-meadows depend on adequate agricultural management to fulfil these important ecological functions. To achieve this in an ecologically and economically sensible way, the prospects for incorporating management and biomass utilization in farming systems appears to be a key issue.

Differences in yield and forage quality in non-intensively managed flood meadows were studied with respect to vegetation type, site conditions, management history, species-richness and nature conservation value. The study covers the most important alluvial grassland communities in the floodplain of the northern Upper Rhine (alliances *Arrhenatherion, Cnidion, Magnocaricion*), which are typically ordered along an elevational gradient of increasing flooding frequency.

Gradients in flooding frequency between the different grassland communities and differences between classes were clearly reflected by floristic composition in Detrended Correspondence Analysis. In contrast, there were only minor differences in terms of soil nutrient status, which are consistent with relatively small differences in yield and forage quality, particularly in the drier *Arrhenatherion* communities. In *Cnidion* meadows, yield and fodder quality were both raised in classes of higher nature conservation value, most likely due to a shift in functional groups towards sedges, herbs and legumes. However, in contrast to hypotheses recently made by several authors, no general relationship between species-richness and productivity was found. We discuss the implications of the results for restoration practice, management strategies and agricultural utilisation of species-rich flood meadows.

Keywords: *Arrhenatherion*, *Cnidion*, Forage quality, Grassland restoration, *Magnocaricion*.

8. 2 Introduction

The devastating floods along several Central European rivers in 2002 (e.g., Elbe, Danube, Moldava) stimulated further discussion on how to best prepare for such events. In this context, the deconstruction of dykes to re-widen the functional floodplain is increasingly discussed as an ecological alternative to more technical solutions such as the upgrading of dykes or the construction of polders for the selective retention of flood peaks (Pfarr & Staeber 1998; Heinken 2001; ICPR 2001). The re-connection of formerly dyke-protected areas will necessarily lead to an increase in flooding frequency, which reduces options of agricultural land-use within the floodplain. Arable use at such sites is fraught with regular total crop loss in the course of floods. Besides alluvial forests, alluvial grasslands are usually the only reasonable land-use option within regularly flooded areas. Such flood-meadows along larger lowland rivers are well adapted to flood disturbance and may tolerate several weeks or even months of submergence (Leyer 2002). Due to nutrient input and favourable moisture supply in the course of floods, they exhibit a relatively high natural productivity. In case of regular management with biomass removal and no additional fertilizer application, they may also act as nutrient sinks along riparian corridors (Rybanic et al. 1999).

Equally, flood-meadows are of high biodiversity conservation value. Certain types of these meadows (e.g. alliance *Cnidion*) are protected by the Fauna Flora Habitat Directive of the European Union (92/43/ECC). They also harbour a number of rare and highly specific plants such as *Arabis nemorensis*, *Cnidium dubium*, *Iris spuria* and *Viola pumila,* which are species of Central European conservation concern (Schnittler & Günther 1999). Due to considerable losses in the past and their high relevance for nature conservation and flood retention, the preservation and restoration of alluvial grasslands is presently one of the major topics in several large-scale floodplain restoration projects along large Central European lowland rivers (Šeffer & Stanová 1999). This also applies to the northern Upper Rhine where, after the opening of dykes, about 300 ha of former arable land have been converted into alluvial grassland during the past two decades (Dister et al. 1992). The former arable land was mostly either left to self-greening or sown with species-poor seed mixtures of common grasses. These meadows and remnant stands of old flood meadows, partly degraded by intense use (i.e. application of fertiliser, two to three cuts per year) were set under protection to improve their floristic quality by non-intensive (i.e. no application of fertiliser, mowing restricted to the time after mid-June) agricultural use as hay meadows. Today the meadows are mown once a year, mostly for hay-production, and a second harvest is only realised in years with exceptionally high precipitation. Currently, the hay is mainly used for feeding of the growing number of leisure horses (DESTATIS 2003). Sheep and cattle play only a minor role in the management of the flood-meadows.

As in many other semi-natural grasslands of high nature conservation value, the organisation of an adequate management emerged as the main challenge in the preservation of this habitat type. However, the interests of farmers and conservationists are often divergent, particularly in terms of raising productivity through fertiliser application, as well as the date and frequency of mowing. The willingness of farmers to accept non-intensive management schemes largely depends on the quantity and quality of the biomass yield. Both aspects are of crucial importance for the marketability and utilization of the harvest as livestock fodder. Whereas several studies have demonstrated the potential and successful incorporation of species-rich and non-intensively managed meadows of mountainous and lowland regions (e.g., Daccord 1990; Jilg & Briemle 1993; Malcharek et al. 1998; Schellberg et al. 1999; Tallowin & Jefferson 1999), only little is known about the possibilities of successfully bringing together interests of agriculture and nature conservation in regularly-flooded alluvial meadows.

In the present study, yield and fodder quality in non-intensively managed flood-meadows was investigated with respect to vegetation type, site conditions and land-use history. Based on these results, the prospects of future incorporation in existing farming and fodder systems have been assessed.

Recent experimental studies gave rise to the controversial claim that high species diversity in grasslands may enhance productivity (e.g., Tilman et al. 1996; Hector et al. 1999). While this assumption is certainly not true in intensively managed grasslands, where high productivity is always coupled with a low species diversity and nature conservation value (Snaydon 1979; Lepš 1999), this may become a relevant factor in non-intensively managed grasslands (Bullock et al. 2001; Schmid 2002), although to date little empirical evidence exists (Grime 2002). Thus, an additional aim of this study was to assess whether there is a link between species-richness and nature conservation value on the one hand and productivity and fodder quality on the other hand. This was done by a comparison of newly-created restoration grassland, degraded and well-preserved target communities.

The following questions are addressed in this article:

- Are there differences in biomass yield and fodder quality with respect to vegetation type and nature conservation value?
- Which factors (site conditions, functional groups, floristic composition, species-richness) are responsible for the observed differences?
- Is it possible to integrate fodder from non-intensive flood-meadows in livestock farming?

8. 3 Material and Methods

Study area

All meadows included in the study are situated in the Hessian portion of the floodplain of the River Rhine about 30 km south-west of Frankfurt, Germany (49°51’ N, 8°23’ E; 80 to 85 m a.s.l.). Site properties are similar to those prevailing along large rivers in continental eastern European lowlands. The climatic conditions are relatively warm and dry, with a mean temperature of 10.3 °C and a mean annual precipitation of 580 mm (Müller-Westermeier 1990). All sites within the Holocene floodplain are directly (flooding) or indirectly (raise of the ground-water table) affected by strong seasonal and inter-annual fluctuations of the water level of the River Rhine, with a maximum amplitude of more than 6 m (Dister 1980; Böger 1991). Calcareous and extremely fine-grained alluvial soils, topping sandy sediments of the Rhine, are predominant over the whole area (Böger 1991). Due to a mostly high clay content (> 60 %) plant-available water declines rapidly during dry and warm periods. These site conditions result in a high variability of soil water potential: While winter, spring and early summer may often bring floods, summers are notably dry. This is also reflected in the occurrence of specialist plants of subcontinental distribution such as *Allium angulosum*, *Cnidium dubium*, *Scutellaria hastifolia* and *Viola pumila* (Hultén & Fries, 1986).

Vegetation types

The 63 meadows under study predominantly belong to the vegetation alliances *Cnidion* ($N = 34$) and *Arrhenatherion* ($N = 25$). For comparative purposes, four *Magnocaricion* stands, dominated by tall sedges, were additionally included. These three alliances are assembled along a gradient of flooding duration. *Magnocaricion* stands occupy the lowest agriculturally used areas of the floodplain, where the average period of inundation of up to 80 days a year caused management to be abandoned in most cases. The more common *Cnidion* meadows occur in areas flooded on average up to 26 days per year, while *Arrhenatherion* meadows are restricted to drier parts of the floodplain submersed on average for less than 8 days per year

(Böger 1991; Hölzel 1999). The hydrologically defined *Cnidion* and *Arrhenatherion* stands were further subdivided into the following classes according to their current floristic composition and nature conservation value, which mostly reflects site conditions and management history: Class **I** comprises young restoration grasslands that developed from former arable land during the past two decades and still lack many common and characteristic species such as *Centaurea jacea* and *Sanguisorba officinalis*. Class **II** comprises old traditional meadows that received intensive agricultural management in the past (use of fertilizer, two to three cuts per year). Floristically they are significantly impoverished in target species. Class **III** comprises old traditional meadows that never received intense management and therefore still harbour a high portion of rare and endangered target species. More details about the species composition of the flood meadows along the northern Upper Rhine can be found in Hölzel & Otte (2003) and Donath et al. (2003).

Sampling of vegetation and biomass

In each studied meadow, the composition of above-ground vegetation was sampled in a randomly placed 100 m^2 quadrate. Species abundance was estimated on a modified Braun-Blanquet scale, which was replaced by a fully numerical 1-9 scale for data analysis (van der Maarel 1979). Plant species nomenclature follows Wisskirchen & Haeupler (1998).

Biomass was collected by harvesting ten 0.1 m^2 square subplots, placed at random within the 100 m^2 plot. According to the regular mowing regime employed in the area, biomass was sampled once in mid June.

Biomass analysis

To determine dry-matter yield, the collected biomass was oven-dried at 60 °C for 48 hours and weighed. Contents of crude protein, crude fibre and crude fat were measured using the NIRS method (Shenk et al. 1989). Spectroscopy (ICP-OES; DIN EN ISO11885) was used to assess contents of phosphorus (P), calcium (Ca), sodium (Na), magnesium (Mg) and potassium (K). As measures for the energy content of the biomass, metabolizable energy (ME) as well as energy for lactation (NEL) in the case of ruminants (Kirchgeßner 1998) and digestible energy (DE) in the case of horses (DLG 1998) was calculated.

Soil-nutrient analysis

Collection of the soil samples was carried out using a soil corer of 3 cm diameter. In each 100 m^2 plot, five cores of 10 cm depth were taken at random locations after removing all plant material from the soil surface. Samples were air-dried, sieved (<2 mm) and extracted with calcium-acetate-lactate (CAL) for the determination of plant-available phosphorus (P) and potassium (K; Hoffmann 1991).

Total nitrogen and total carbon content were analysed with a CN-Analyser (FlashEA 1112, Thermoquest). Total carbon and the content of $CaCO_3$, which was analysed according to the method of Scheibler (Hoffmann 1991), were used to calculate the C/N-ratio as a measure for nitrogen availability (Kuntze et al. 1994).

Data analysis

From vegetation samples, cover-weighted means of the Ellenberg values for moisture (MV) and nitrogen (NV) were derived as indirect measures for the water and nutrient supply (Ellenberg et al. 1991). To assess the influence of different functional groups on forage quality and yield in each sample, the respective coverage of *Poaceae*, *Cyperaceae*, *Fabaceae* and herbs without *Fabaceae* was determined.

Detrended Correspondence Analysis (DCA) was used to explore gradients in the floristic composition of vegetation samples of *Cnidion* and *Arrhenatherion* meadows. To reduce their unduly influence on ordination results, species with less than three occurrences were omitted from the data matrix, which left 113 species in the analysis. DCA-ordination revealed a total inertia of 3.18 and the gradient length of the first axis was 3.37, which made it appropriate to use a unimodal model (Ter Braak & Smilauer 1998). According to the after-the-fact evaluation, the two axes accounted for 44.9 % and 7.9 %, respectively, of the variance in the original data set (McCune & Mefford 2002).

To test for differences in site, vegetation and forage quality parameters, the Tukey´s Honest-Significance test (HSD) for unequal sample size post-hoc an ANOVA was employed (Spjotvoll & Stoline, 1973). Percentages were subjected to angular transformation prior to analyses (Zar 1999).

Correlations between site, vegetation and hay content parameters were analysed by non-parametric Spearman rank correlation. Since the different measures for energy (i.e. ME, NEL, DE) are highly correlated, only ME was included in the correlation matrix.

Statistical analyses and correlations were performed with the software package STATISTICA 6.0 (Anon. 2002a). DCA and the related statistical procedures were carried out with PC-Ord 4.14 (McCune & Mefford 1999).

8. 4 Results

Vegetation and site conditions

DCA-ordination revealed an overall separation between *Cnidion* and *Arrhenatherion* meadows along axis 1, which had a high correlation with Ellenberg moisture value (r = 0.78; Figure 1). The respective classes were separated along axis 3, which represented a nutrient gradient (r = -0.49). This separation is most prominent between class I meadows on the one hand and class II as well as target communities (class III) on the other hand.

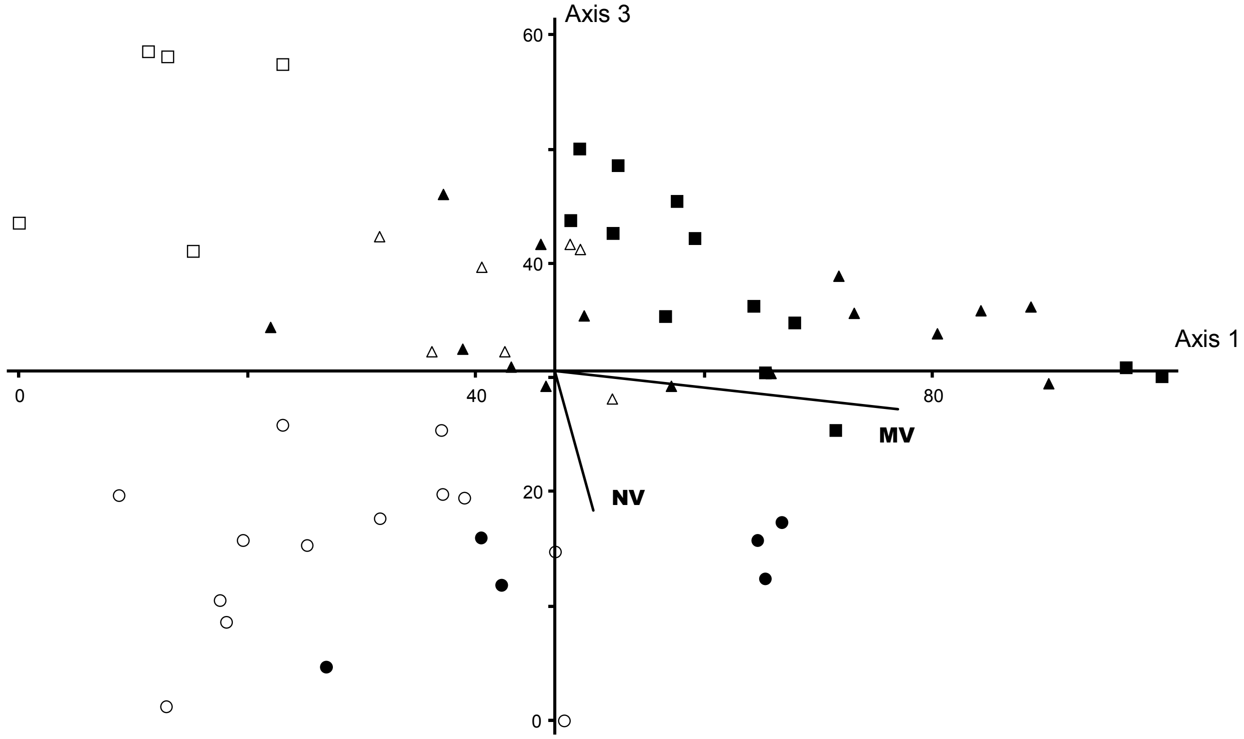

Figure 1. DCA-ordination diagram with scores of all relevés along axis 1 and 3. Filled symbols represent meadows of the alliance *Cnidion*, empty symbols of the alliance *Arrhenatherion*. Different symbols represent meadows of class I (circles), of class II (triangles) and class III (squares). Vectors represent the Ellenberg moisture value (MV) and the Ellenberg nitrogen value (NV).

Comparison of vegetation and site parameters between classes within *Arrhenatherion* and *Cnidion* meadows revealed significantly higher species numbers and lower Ellenberg nutrient values in the target communities (class III), but trends in plant-available nutrients and Ellenberg moisture value were not significant (Table 1). Only in the case of *Cnidion* meadows were changes in proportion of functional groups (i. e. *Poaceae*, herbs and *Fabaceae*) between classes confirmed. All other compositional differences in *Arrhenatherion* and *Cnidion* meadows were not significant.

Tests for differences in site parameters (α = 0.05) between the class III of *Arrhenatherion*, *Cnidion* and *Magnocaricion* stands showed that only the Ellenberg moisture value was significantly different between all three communities and contents of plant-available potassium were significantly highest in *Magnocaricion* meadows. While the proportion of *Cyperaceae* were highest in *Magnocaricion* meadows, in these stands the proportions of *Poaceae* and *Fabaceae* as well as total species number was significantly lowest (Table 1).

Table 1. Comparison of vegetation, soil and site parameters between classes of *Arrhenatherion* and *Cnidion* meadows.

Class	*Arrhenatherion*						*Cnidion*						*Magnocaricion*	
	I (N = 13)		**II** (N = 7)		**III** (N = 5)		**I** (N = 6)		**II** (N = 15)		**III** (N = 13)		**III** (N = 4)	
	x	***se***	***x***	***se***	***X***	***se***	***x***	***se***	***x***	***se***	***x***	***se***	***x***	***se***
Species Number	23.7^{a}	1.7	20.0^{a}	2.5	$_{a}33.6^{b}$	2.2	20.8^{a}	1.3	23.7^{a}	1.6	$_{a}33.1^{b}$	1.8	$_{b}18.75$	0.48
Poaceae (%)	69.8	2.3	76.5	5.5	$_{a}70.3$	4.9	81.2^{a}	5.2	59.0^{a}	4.5	$_{a}52.4^{b}$	5.1	$_{b}9.44$	0.42
Cyperaceae (%)	0.5	0.3	2.4	1.0	$_{a}0.7$	0.7	3.4	2.1	8.4^{b}	2.1	$_{a}11.5$	4.3	$_{b}49.28$	6.80
Herbs (%)	24.2	2.6	16.1	4.0	21.0	4.5	14.9^{a}	4.2	30.4^{b}	2.7	31.4^{b}	12.8	41.08	6.54
Fabaceae (%)	3.9	1.4	4.5	2.0	$_{a}6.4$	1.7	0.3^{a}	0.1	1.3^{a}	0.3	$_{a}4.0^{b}$	0.6	$_{b}0.15$	0.09
C/N-ratio	10.5	0.2	11.2	0.5	10.8	0.2	9.8	0.5	11.2	0.2	10.6	0.4	11.17	0.01
P (mg $100g^{-1}$)	7.3	1.1	6.3	1.9	$_{a}6.1$	1.8	6.3	1.2	5.9	1.2	$_{a}4.0$	1.0	$_{b}8.47$	1.84
K (mg $100g^{-1}$)	11.7	0.8	8.5	0.8	$_{a}8.3$	0.8	8.0	1.0	9.7	0.5	$_{a}8.7$	0.6	$_{b}12.46$	0.57
NV	5.5^{a}	0.1	5.4^{a}	0.2	4.5^{b}	0.3	5.7^{a}	0.1	5.6^{a}	0.1	4.9^{b}	0.2	5.13	0.14
MV	5.3	0.1	5.3	0.2	$_{a}4.6$	0.2	6.5	0.2	5.7	0.2	$_{b}6.3$	0.2	$_{c}8.68$	0.11

Different letters in superscript indicate significant differences ($\alpha = 0.05$) between classes I-III within each vegetation type, whereas different letters in subscript indicate significant differences between meadows of classes III as revealed by the Tukey Honest-Significance test (HSD) for unequal sample size performed post-hoc a significant ANOVA. *x* = mean; *se* = standard error of mean; NV = Ellenberg nitrogen value, MV = Ellenberg moisture value.

Yield and fodder quality

As in the above traits, the classes in *Cnidion* meadows showed more significant differences in parameters of forage quality than *Arrhenatherion* meadows (Table 2). In the latter, only crude protein and phosphorus content in harvested biomass revealed significant differences. This was also true in *Cnidion* meadows but additionally the significantly higher crude protein contents in class II and III meadows were accompanied by higher crude fat and lower crude fibre contents. While measures of energy content for ruminants (i.e. ME, NEL) were both significantly higher in species-rich stands (class III), measures for energy content used in horse feeding (DE) showed no significant differences. Among the *Cnidion* meadows yield and content of Mg differed significantly only between meadows of class I and III, respectively, between class II and III.

Table 2. Comparison of yield and forage quality between classes of *Arrhenatherion* and *Cnidion* meadows harvested in mid-June.

	Arrhenatherion						*Cnidion*						*Magnocaricion*	
Class	**I**		**II**		**III**		**I**		**II**		**III**		**III**	
	(N = 13)		(N = 7)		(N = 5)		(N = 6)		(N = 15)		(N = 13)		(N = 4)	
	x	***se***	***x***	***se***	***x***	***se***	***x***	***se***	***x***	***se***	***x***	***se***	***x***	***se***
Yield (g m^{-2})	421.1	16.8	481.7	25.4	406.2	39.6	353.0^{a}	24.5	455.5^{a}	21.0	468.8^{b}	19.6	550.5	123.4
C-protein (g kg^{-1})	67.2^{a}	3.1	83.0^{b}	4.3	74.9^{ab}	4.7	58.3^{a}	3.6	81.8^{b}	4.3	83.9^{b}	4.5	89.7	11.3
C-fibre (g kg^{-1})	350.8	4.7	339.2	5.7	${}_{a}355.5$	9.1	338.2^{a}	4.8	326.0^{a}	4.6	${}_{b}305.9^{b}$	8.0	${}_{ab}311.2$	7.9
C-fat (g kg^{-1})	16.1	0.8	19.7	0.9	17.6	1.5	16.0^{a}	0.8	20.8^{b}	0.9	20.2^{ab}	1.0	17.1	0.7
P (g kg^{-1})	2.5^{a}	0.1	2.2^{ab}	0.1	1.8^{b}	0.2	2.4^{ab}	0.2	2.4^{a}	0.1	1.8^{b}	0.1	1.9	0.2
Ca (g kg^{-1})	5.9	0.3	5.5	0.2	${}_{a}5.0$	0.3	5.3	0.2	5.9	0.3	${}_{ab}7.0$	0.4	${}_{b}8.8$	1.1
Na (g kg^{-1})	0.2	0.02	0.3	0.1	0.3	0.1	0.4	0.1	0.2	0.02	0.3	0.1	0.4	0.04
Mg (g kg^{-1})	1.6	0.1	1.7	0.1	${}_{a}1.5$	0.1	1.5^{ab}	0.1	1.6^{a}	0.1	${}_{b}2.0^{b}$	0.1	${}_{ab}1.7$	0.1
K (g kg^{-1})	18.8	0.6	18.7	1.2	15.8	1.1	16.9	1.3	20.9	1.6	20.1	1.2	18.6	0.4
ME (MJ kg^{-1})	8.80	0.08	8.99	0.11	${}_{a}8.82$	0.13	9.01^{a}	0.07	9.2^{ab}	0.06	${}_{b}9.49^{b}$	0.11	${}_{b}9.48$	0.11
NEL (MJ kg^{-1})	5.09	0.05	5.23	0.07	${}_{a}5.10$	0.09	5.23^{a}	0.05	5.38^{ab}	0.04	${}_{b}5.57^{b}$	0.08	${}_{b}5.56$	0.08
DE (MJ kg^{-1})	9.46	0.01	9.49	0.07	${}_{a}9.52$	0.04	9.58	0.04	9.58	0.03	${}_{ab}9.65$	0.03	${}_{b}9.7$	0.01

Different letters in superscript indicate significant differences ($\alpha = 0.05$) between classes I-III within each vegetation type, while different letters in subscript indicate significant differences between meadows of classes III as revealed by the Tukey Honest-Significance test (HSD) for unequal sample size performed post-hoc a significant ANOVA. x = mean; *se* = standard error of mean; C- = crude-; NEL = net energy for lactation; ME = metabolizable energy; DE = digestible energy.

Comparison between the three target communities (class III) only showed significantly higher values of ME and NEL in *Cnidion* and *Magnocaricion* meadows compared to *Arrhenatherion*-stands, while DE was only significantly different between *Magnocaricion* and *Arrhenatherion* meadows. Crude fibre and Mg contents of the forage revealed significant differences only between target communities of *Cnidion* and *Arrhenatherion* meadows. Ca content in biomass from *Magnocaricion* meadows was only significantly raised compared to *Arrhenatherion*-meadows. All other tested variables, including yield, showed no significant differences between meadows of class III.

Relationship between fodder quality, vegetation and site parameters

In correlation analysis, *Arrhenatherion* stands generally showed only few significant correlations, but in *Cnidion* meadows yield, protein, fat and energy (ME) had in all but two cases a significantly positive, and fibre a significantly negative correlation with the proportion of *Cyperaceae*, herbs and *Fabaceae* (Table 3). Opposite trends were revealed for *Poaceae*. Species number in *Cnidion* meadows was negatively related to the proportion of *Poaceae* and positively to the proportion of herbs and *Fabaceae*. In *Arrhenatherion* meadows analogous relations held true only for the proportions of *Poaceae* and herbs. While in both meadow types the correlation between species number and Ellenberg nutrient value was significantly negative, its relation to yield was significantly positive only in case of the *Cnidion* meadows but negative in *Arrhenatherion* meadows.

Table 3. Matrix of Spearman-Rank Correlations for relationships between vegetation, site and fodder quality parameters of *Cnidion* ($N = 34$) and *Arrhenatherion* meadows ($N = 25$).

	Species no.	Yield	C-protein	C-fibre	C-fat	ME
Cnidion meadows						
Species number	--	**0.36**	**0.37**	-0.30	0.22	**0.34**
Poaceae (%)	**-0.60**	**-0.46**	**-0.66**	**0.55**	**-0.61**	**-0.57**
Cyperaceae (%)	0.19	**0.41**	**0.46**	**-0.34**	**0.53**	0.32
Herbs (%)	**0.56**	0.25	**0.48**	**-0.40**	**0.40**	**0.40**
Fabaceae (%)	**0.55**	**0.34**	**0.51**	**-0.37**	**0.34**	**0.39**
NV	**-0.55**	-0.01	-0.09	0.04	0.14	-0.07
Arrhenatherion meadows						
Species number	--	**-0.42**	-0.10	0.12	-0.10	0.01
Poaceae (%)	**-0.57**	0.18	0.13	-0.14	0.35	0.12
Cyperaceae (%)	0.03	-0.20	-0.16	-0.10	0.24	0.15
Herbs (%)	**0.52**	-0.22	-0.26	0.06	-0.29	-0.07
Fabaceae (%)	0.18	0.13	0.01	0.27	-0.29	-0.23
NV	**-0.43**	0.00	-0.37	-0.04	-0.01	-0.09

Functional groups (*Poaceae*, *Cyperaceae*, Herbs and *Fabaceae*) were included in the correlations with their relative contribution to the total abundance. Significant correlations at an α-level of 0.05 are given in boldface. Units and abbreviations as given in Tables 1 and 2.

8. 5 Discussion

Influence of site and vegetation parameters

The DCA-Ordination confirmed a clear split between *Arrhenatherion* and *Cnidion* meadows along a moisture gradient (axis 1) and a separation of the classes along a nutrient gradient (axis 3; Figure 1). This negative correlation between Ellenberg's nutrient value, the nature conservation value and species richness is consistent with other studies (Gough & Marrs 1990; Smith 1993; Oomes et al. 1996; Critchley et al. 2002). Yield and parameters of forage quality, on the other hand, should positively correlate with increasing nutrient availability, however no such trend was found in the present study (Table 3). In contrast to other experimental studies (e.g., Schellberg et al. 1999) the range of soil nutrient status was small. These differences in soil nutrient status in *Arrhenatherion* as well as *Cnidion* meadows (Table 1) were not only insignificant but, consistent with results from an earlier study (Donath et al. 2003) were also too small to be agriculturally and ecologically relevant. While patterns of nutrient and water supply in *Arrhenatherion* meadows are consistent with insignificant changes of yield and forage quality, they do not explain the increase in yield and quality parameters in *Cnidion* meadows from classes I to III (Table 2). Only the significantly higher energy contents in target communities (class III) of *Cnidion* and *Magnocaricion* stands, and the albeit not significant increase in yield from *Arrhenatherion* to *Magnocaricion* meadows may be explained by a slightly better water supply (Table 1, c.f. Jakrlová 1999).

Much stronger was the relationship revealed by correlation analysis between biomass yield and forage quality to floristic composition and functional groups, respectively (Table 3). The strong positive impact of *Cyperaceae*, *Fabaceae* as well as herbs on fodder quality found in *Cnidion* meadows may be a result of different traits which species in these groups have in common. Herbs and legumes not only contribute to quality and acceptance of forage, they also enlarge the time frame in which good quality hay (i.e. lower crude fibre, higher crude protein and energy content) can be obtained (Lehmann et al. 1985; Opitz v. Boberfeld & Theobald 2003). The same appears to be true for sedges, which similar to herbs typically exhibit relatively long-lived leaves (Grime et al. 1988), while in grasses senescence and quality decrease (i.e. increase of crude fibre and decrease of crude protein) already set in with the growth of the inflorescence. *Carex* species also seem to take advantage of their special adaptation to capture phosphorus, which often limits growth in the calcareous soils that are predominant over the whole study area (Grime 2002). Additionally, losses in yield due to low nutrient availability are compensated for by *Fabaceae* through their ability to fix nitrogen (Klapp 1965; Hector et al. 1999). Since in *Arrhenatherion* meadows the proportion of

Fabaceae and *Cyperaceae* was more similar across the different classes (Table 1), and in contrast to *Cnidion* meadows high-yielding sedges such as *Carex disticha* and *C. acutiformis* were missing, their impact on yield and fodder quality was much smaller.

This corresponds to results of an experiment in calcareous pastures by Booth and Grime (Grime 2002) where the inclusion of high-yielding sedges was shown to be the main reason for increased yield in some species-rich plant communities. Consequently, this study also could not confirm a general rule for a positive relationship between species-richness and biomass production (e.g., Tilman et al. 1996, Hector et al. 1999). The high importance of species composition and proportion of functional groups on yield and forage quality resulted in diametrical trends when analysing the influence of species-richness on yield in *Arrhenatherion* and *Cnidion* meadows (Table 3). In addition, *Magnocaricion* meadows showed the significantly lowest number of species although they had the highest yield (Table 1, 2). In general, there is little evidence that species richness enhances productivity (Grime 2002), especially in meadows under intensive agricultural management (Fridley 2001). In highly productive systems Bakker (1989) highlighted the importance of cutting date. In such systems species number was only enhanced through cutting in July, whereas in systems with lower productivity late mowing resulted in a higher species number. In general, in meadows with relatively high productivity, regular cutting at the first peak of standing crop seems to at least partly compensate the tendency towards competitive exclusion of less competitive herbs (Huston 1994; Grace 2001). Additionally, Osem et al. (2002) found that removing biomass through grazing had a positive effect on species richness, through lowering competitive exclusion, but only in productive stands of herbaceous annual vegetation. This mechanism may explain why the relatively high-yielding, regularly mown *Cnidion* meadows showed a positive relationship between species-richness, productivity and fodder quality (i.e. crude protein, ME).

Generally, the results strongly suggest that there will be no decline in yield and forage quality in the course of the ongoing restoration of target communities. Yet, in accordance with Snaydon (1979) little evidence was found that species-enrichment would lead to an agriculturally noteworthy increase in productivity compared to other factors such as variability of weather conditions and the strong effects of fertilization.

Integration in feeding systems

A comparison of the obtained results (Table 2) with nutrition tables from the German Agricultural Society and the U.S. Nutrition Research Council for horses (NRC 1989; DLG 1998), cattle and sheep (DLG 1997; NRC 2001) suggests that the hay from flood-meadows can be suitably incorporated in feeding systems as basic ration. This is in accordance with Franke (2003) who, as in the present study, found that biomass with similar date of harvest tended not to reach energy levels of high quality forages (NEL > 6 MJ kg^{-1} DM^{-1}), but should in most cases be sufficient to fulfil basic requirements of cattle and horses. Typically, hay from species-rich meadows also had the lowest contents of P (Tallowin & Jefferson 1999) and as a characteristic of natural feedstuff, Na concentrations are below adequate levels for cattle and horses (Jarrige & Martin-Rosset 1981; NRC 2001). Contents of all other minerals included in this study are within the range of minimum requirements of basic rations. Especially in life-periods with higher demands on forage quality, however, e.g. gestation, lactation, growing or hard work, hay from non-intensive flood-meadows alone will not always supply the necessary amounts of energy, protein and other ingredients. In these cases high quality fodder and adequate supplementation will be necessary (NRC 2001; Meyer & Coenen 2002).

In general, the harvested hay is more easily incorporated in feeding-systems for horses, which can more easily compensate lower forage quality by higher daily intake (Duncan et al. 1990; Menard et al. 2002). Even when quality parameters of hay from species-rich meadows proscribe the use as basic fodder, there is still the possibility to substitute the use of straw as fibre supply in the high-energy fodder rations of cattle (Jilg & Briemle 1992; NRC 2001).

In the present study, higher proportions of sedges were not related to decreasing energy contents (Table 3). Similar results were found by Franke (2003) in alluvial meadows of the Elbe river, where early-cut swards dominated by broad-leaved sedges (e.g. *Carex vulpina*) still reached high quality (NEL > 6 MJ/kg DM). These findings, along with the good acceptance of broad leaved sedges in hay by ruminants and in particular horses (Franke 2003; local farmers - personal communication), bring into question the negative rating of swards with high portions of sedges (Klapp 1965; Jakrlová 1999).

Conditions of grassland management

In contrast to other grassland communities with high nature conservation value but low productivity (e.g. meso-xerophytic grassland), flood-meadows exhibit relatively high harvests even without soil improvement or re-seeding with high yielding cultivars, as is regularly employed in intensive grassland management (Tallowin & Jefferson 1999).

Besides relatively high yields and good forage quality other factors also benefit agricultural management of flood-meadows in an economically sensible way: i) Flood-meadow allotments usually comprise several hectares of level surfaces that do not hamper the use of modern, highly efficient harvesting machinery; ii) In contrast to permanently wet grasslands, often exhibiting soft and instable soils, no specially adapted machinery is needed due to the rapid hardening of soils from late spring onwards; iii) The usually dry and warm weather conditions during the harvest period minimize the work-load for hay drying and guarantee high fodder quality.

However, divergent interests of farmers and conservationists remain the most serious problem. Farmers are interested in high yields of high quality whereas conservationists on the other hand demand management regimes that support floristic and faunistic diversity. Endangered ground-nesting meadow birds, which are often the cause of restrictive guidelines for mowing dates, traditionally do not play a prominent role in the studied meadows. Although often regarded as sensitive towards early mowing (Briemle and Ellenberg, 1994) the majority of the target plant species have been shown to tolerate a first cut in June by their high abundance in meadows that received such management for decades (Hölzel 1999; Leyer 2002). Most of these species boast an aptitude for successful vegetative regeneration or flowering and seed production during the second growth in late summer. In terms of plant species diversity there is no urgent need for a delayed first cut that considerably diminishes forage quality. Kirkham and Tallowin (1995) also found that cutting date inflicted only small changes in species with predominantly vegetative regeneration in meadows on the Somerset Levels. This suggests that only species lacking both a vegetative regeneration strategy and the ability to produce seeds after a first cut depend from time to time on a late first cut to successfully reproduce by seeds. However, since restrictive management guidelines with a late first cut inflict a considerable loss in forage quality (Tallowin & Jefferson 1999) more flexible management schemes should generally be employed and evaluated.

Conclusions

The prerequisites for a successful integration of the studied flood-meadows in existing farming systems are particularly favourable. This applies not only to the natural conditions of production but also to the position of the study area at the outskirts of the Rhine-Main agglomeration, one of Europe’s economically most prospering regions. The steadily increasing stock of leisure horses has given farmers the opportunity to diversify their income by horse-keeping. Indeed, some farmers actually specialise in the marketing of high quality hay from flood-meadows for race and leisure horses. Additionally, hay exports to neighbouring countries such as Switzerland and The Netherlands implies that long-distance transport does not preclude such management alternatives in peripheral regions.

In accordance with other studies (c.f. Tallowin & Jefferson 1999; Franke 2003), the findings suggest that farmers and conservationists' interests can be brought together. Such studies are of growing importance in assisting conservationists to convince farmers to manage grasslands non-intensively without public compensation payments. In contrast to widespread prejudice among farmers, the study shows that yield and fodder quality may be surprisingly high in non-intensively managed grasslands. Equally, it has been established that under non-intensive management and increasing nature conservation value, forage yield and quality will not necessarily decrease but may even improve in some meadow types.

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9 General discussion

The impact of site conditions and dispersal

The assessment of restoration success ten years after the start of restorative measures showed that suitable abiotic site conditions are no guarantee for the re-establishment of target species and communities (chapter 5). As in other studies, dispersal limitation of target species in combination with their low potential to build up long-term persistent seed-banks was revealed as the most serious limiting factor (cf. Bakker & Berendse 1999). While viable remnant populations of target species in the vicinity of restoration sites are crucial for species-enrichment at the target sites, they are not sufficient. Even if such remnant stands are found, the species are only able to bridge short distances and most newly emerged individuals in the study area are found close to the remnants along ditches and paths. In the few cases where re-colonisation of meadows by target species took place this was related only to the presence of source populations along ditches but not to the species occurrence on neighbouring meadows. This is due to low capacities of seeds for long distance dispersal, even if these are wind-dispersed (Jongejans & Telenius 2001, Bischoff 2002). This dispersal limitation can not be compensated by water dispersal at sites freely accessible to floods of the Rhine (Bissels et al. 2004b), which is in contrast to findings along smaller, more rapidly running and less confined rivers where this process proved to be quite successful (Bonn & Poschlod 1998, Boedeltje et al. 2004, Vogt et al. 2004). Additionally, under present-day conditions, traditional agricultural dispersal processes, such as haymaking (Strykstra et al. 1997) and aftermath grazing (Fischer et al. 1996), are not effective in spreading seeds.

In conclusion, even under favourable conditions, dispersal and establishment of target species seems to be an uncertain and time-consuming process. Management of remnant populations and target areas, time and active enhancement of seed dispersal are the main agents that strongly influence restoration success in terms of species enrichment. Therefore, management has to be adjusted with the aim of keeping viable populations of target species, since these are the only substantial local seed source of certain species that may ensure at least short-distance seed dispersal.

Significance of soil seed bank

While in chapter 5 only an indirect assessment of the potential of the seedbank was possible, the analysis of seedbanks in low lying arable fields, holding species-rich flood meadows in the past (Knapp 1954; Krug 1997), made a direct evaluation feasible (chapter 6). This analysis confirmed that the re-establishment of flood meadow communities from the seedbank is not possible since seeds of grassland species are almost totally lacking. This is in accordance with findings that seed banks are almost completely depleted after years of arable cultivation or intensive grassland management (cf. Bakker 1989; Pfadenhauer & Maas 1987; Thompson et al. 1997).

In contrast, the seedbank was revealed to be highly important for the preservation of another group of endangered species, i.e. those of ephemeral wetlands. Since both, flood meadows and ephemeral wetland vegetation, are found under similar site conditions but under different management, conflicts may arise in the course of grassland restoration projects. But while it is quite unlikely that all secondary habitats of ephemeral wetland vegetation will be included into restoration projects, the most important threats to these communities are inappropriate agricultural management schemes. In these dynamic habitats, seedbanks are of major importance for the long-term preservation of such ephemeral wetland plant communities. Measurements for their preservation have to aim at the maintenance and renewal of the seedbank. Mudflat plants in primary habitats, i.e. along rivers, are able to grow and reproduce also in years with only slight drawdown at exposed edges of oxbows and river banks. In secondary habitats, on the other hand, successful reproduction and thus replenishment of the soil seedbank is restricted to years with extremely long lasting floods of the Rhine. Thus, reproduction is not only a priori less frequent than in primary habitats, but additionally at risk by human activities. Since farmers want to reduce the losses in crops caused by inundation of fields they try to lower flooding frequency and duration by improved drainage or by landfill depressions with soil, which means a complete destruction of the habitat for wetland ephemerals (Täuber & Petersen 2000).

Microsite limitation

In the study area neither seedbanks nor seed dispersal proved to be capable to enhance re-colonisation by target-species in flood meadow restoration. Hence, the active introduction of seeds seems to be a promising alternative (Hölzel & Otte 2003). In this context it is important to know how different treatments affect seedling establishment (chapter 7).

While the disturbance of a dense sward facilitated seedling recruitment in almost all study species, the effects of litter and simultaneously sown grass seemed to be more species specific. An increase in germination in the presence of litter may be due to constantly higher moisture which probably breaks physical dormancy of hard seed shells, through a higher exposition to microbiological activity below litter (e.g., Baskin & Baskin 2001). Also in the phase of early establishment positive effects of litter on survival can be attributed to a higher and less variable moisture regime below it (Xiong & Nilsson 1999; Eckstein & Donath, submitted). In contrast, the two species with the smallest seeds, i.e. *Arabis nemorensis* and *Pseudolysmachion longifolium*, almost completely failed to germinate from below the litter cover. In general, in small seeded species there was probably a strong selection against dark germination, since they lack the reserves needed to break through a litter or soil cover (Hodkinson et al. 1998; Bosy & Reader 1999; Turnbull et al. 1999; Milberg et al. 2000; Baskin & Baskin 2001). In consequence, in restoration projects aiming at species-enrichment through application of seed-containing plant material from species-rich flood meadows (cf. Hölzel & Otte 2003) it may be reasonable to avoid a strictly homogenous and unstructured spread of the material. This will result in a variety of germination niches and increase the chance that particular germination requirements of a wide variety of species are met.

In contrast to the negative impact of a dense sward on seedling recruitment (Gross & Werner 1982; Goldberg & Werner 1983; Kotorová & Leps 1999), annuals and other short lived ruderals dominating early successional stages are usually not hampering the reestablishment of introduced target-species (Bosshard 1999; Pfadenhauer & Miller 2000). In this context, the finding in chapter 7, that - in contrast to a dense sward - simultaneously sown grass did not negatively affect seedling recruitment in target species highlighted the greater importance of dispersal limitation compared to microsite limitation in the study area. The effects may be seen as a consequence of the simultaneous development of the sown grasses and herbs in the former arable fields. By the time the grasses would have lowered incidence of light to levels, at which germination is reduced (Foster & Gross 1998; Jutila & Grace 2002) most of the emergence of sown herbs had already taken place. The same seems to be true in case of below-ground competition, which potentially hampers rooting of seedlings for water and nutrient uptake but at this early developmental stage the root system can be expected to be low. Consequently, the results suggested that the presence of safe sites, which are essential for successful emergence of seedlings (Grubb 1977), was not significantly narrowed by the sown grass.

No evidence was found that rare species are especially particular in their requirements for seedling recruitment. *Iris spuria*, the rarest of the study species, was at all experimental sites among the most successful species with much higher or at least similar establishment rates as *Silaum silaus*, the least endangered species.

Beyond species specific differences, there seems to be a sensitive balance between the different environmental factors influencing recruitment success, which concurs with theoretical considerations of non-equilibrium conditions (Huston 1994). Species can circumvent unfavourable site conditions either by building up a long-term persistent seedbank, which in grasslands is done only by a small portion of species (e.g., Hölzel & Otte 2004a), or by vegetative persistence in combination with generative reproduction. In the latter case, also rare events of successful seedling recruitment will be sufficient to maintain a viable population stage structure (Bissels et al. 2004a).

In general, the naturally occurring variation of site conditions had a greater impact especially on survival and establishment success than treatments that mimicked restoration measures. As a consequence, success in restoration of species-rich flood meadows may be enhanced, if the introduction of seeds at a site is done several years in a row to circumvent unfavourable conditions for seedling recruitment in one specific year.

Utilisation of biomass

In the context of an ongoing restoration project along the northern Upper Rhine the finding in chapter 7, that - in contrast to a dense sward - simultaneously sown grass did not hamper seedling recruitment may ease the task of bringing together interests of farmers and conservationists. Through sowing of grass, restored grasslands will faster yield hay quantities and qualities worth harvesting, accelerating their integration into local farming systems, which is urgently needed to maintain the newly created diversity.

In general, biomass from alluvial meadows along the northern Rhine proved to be suitable for incorporation in local farming systems. As in flood meadows along the River Elbe quality parameters were surprisingly high, although they did not reach highest quality levels (Franke 2003). Due to the relatively high content of fibre, biomass from non-intensively managed grasslands should preferentially be incorporated into feeding systems for horses. However, for animals in phases of the life cycle with higher demands on forage quality, e.g. during gestation, lactation, growing or during periods of hard work, the incorporation of hay from non-intensive flood-meadows will need special attention of farmers to ensure the necessary amounts of energy, protein and other ingredients for the livestock (Tallowin & Jefferson 1999).

Interestingly, high nature conservation value of flood meadows did not preclude incorporation into farming systems (chapter 8). Instead, quantity and quality of biomass of *Cnidion*-meadows was lower in newly created, grass dominated meadows compared to old, herb-rich meadows. Since the opposite was true in case of the *Arrhenatherion*-meadows, the study could not confirm the general claim of Hector et al. (1999) that biomass yield increases with diversity. The patterns found are more likely due to species specific traits. With respect to quality parameters the different portions of herbs in *Cnidion*-meadows of different nature conservation value are the reason for elevated quality in herb-rich meadows. This is owed to the later onset of senescence in herbs compared to grasses, which prolongs the timeframe in which good quality hay can be obtained (Grime et al. 1988; Lehmann et al. 1985).

Beyond these positive prospects for the agricultural incorporation of flood-meadows, the results also draw attention to the fact that typical flood meadow species cope well with the traditional management regime in the area, i.e. one to two cuts a year for hay making. Although many target plant species of flood meadows are regarded to be negatively affected by early mowing (Briemle and Ellenberg 1994), high abundance of these species in meadows that received such management for decades indicates that the majority of the floodplain species under study tolerate a first cut in June (Hölzel 1999; Leyer 2002). Most of these species are capable of successful vegetative regeneration or flowering and seed production during the second growth in late summer even after an early first cut. This suggests that only species lacking both a vegetative regeneration strategy and the ability to produce seeds after a first cut depend on a late first cut at least from time to time to successfully reproduce by seeds. However, since restrictive management guidelines with a late first cut inflict a considerable loss in forage quality (Tallowin & Jefferson 1999) flexible management schemes should be more often considered and employed.

10 Deutsche Zusammenfassung

Die vorliegende Arbeit „Renaturierung von Auenwiesen – die Bedeutung der Samenbank, Ausbreitung, Etablierung und landwirtschaftlichen Nutzung“ behandelt folgende Fragestellungen:

i. In welchem Maße findet eine Wiederbesiedlung ehemaliger Äcker und artenverarmter Grünlandflächen durch seltene Auenwiesenarten statt (Kapitel 5)?
ii. Welchen Beitrag kann die auf Ackerflächen vorzufindende Bodensamenbank zur Renaturierung artenreicher Auenwiesen leisten (Kapitel 6)?
iii. Welchen Einfluß haben verschiedene Behandlungen, wie sie auch bei der Umsetzung von Renaturierungsmaßnahmen eingesetzt werden, auf die Keimung und Etablierung von Zielarten (Kapitel 7)?
iv. Welche Möglichkeiten bestehen, die artenreichen Auenwiesen in die lokalen landwirtschaftlichen Strukturen einzubinden und Haupteinflussfaktoren dafür (Kapitel 8)?

In einem abschließenden Kapitel wird diskutiert, welche Schlussfolgerungen aus den Ergebnissen der durchgeführten Untersuchungen für die Renaturierung artenreicher Auenwiesen gezogen werden können (Kapitel 9).

Alle Untersuchungen im Rahmen der vorliegenden Arbeit wurden im hessische Ried entlang des hessischen Oberrheins durchgeführt. Der Lebensraum, der im Untersuchungsgebiet vorkommenden Ausprägung der Auenwiesen (Stromtalwiesen), zeichnet sich durch einen starke Variabilität im Gehalt an pflanzenverfügbarem Wasser aus. Phasen des Wasserüberschusses, während der regelmäßig im Winter, Frühling und Frühsommer auftretenden Hochwasserereignisse des Rheins, wechseln mit Phasen stark reduzierter Gehalte an pflanzenverfügbarem Bodenwasser im Sommer ab. Letzteres ist zum einen auf die hohen Tongehalte der Böden (>60 %), mit geringer Kapazität für pflanzenverfügbares Wasser, zum anderen auf die relativ geringen mittleren jährlichen Niederschlagsmengen (580 mm) bei einer gleichzeitig relativ hohen mittleren Jahrestemperatur von 10.3°C zurückzuführen. Diese hydrologischen, edaphischen und klimatischen Besonderheiten ähneln Bedingungen, die entlang großer, osteuropäischer Stromtäler vorherrschen. Daher erreichen einige der für die Stromtalwiesen typischen Arten (z. B. *Allium angulosum*, *Scuttelaria hastifolia*) am hessischen Oberrhein die Westgrenze ihres Areals.

Das Untersuchungsgebiet wird durch Sommer- und Winterdeich in drei hydrologische Kompartimente unterteilt: i) Die Rezentaue rheinseits der Sommerdeiche wird direkt von sedimenttragendem Rheinwasser während Hochwasserereignissen überflutet. ii) Die Hybridaue zwischen Sommer- und Winterdeich dagegen wird nur überflutet während Hochwasserereignissen, welche die Marke von 4 m über Mittelwasser überschreiten. iii) Im Bereich der Altaue, landseits des Winterdeichs, werden tiefliegende Bereiche durch klares aufsteigendes Grundwasser überstaut, welches durch hydrostatischen Druck während Hochwasserereignissen des Rheins aufsteigt.

Bis in die fünfziger und sechziger Jahre des letzten Jahrhunderts wurde das Gebiet von artenreichen Auenwiesen geprägt, welche traditionell als Heuwiesen genutzt wurden. Agrarstruktureller Wandel, zunehmende Drainage tiefliegender Flächen und eine Folge trockener Jahre begünstigten die Umwandlung weiter Teile der Grünlandbestände im Untersuchungsgebiet in Ackerland. Als Folge waren zu Beginn der achtziger Jahre nur kleine, isolierte Restbestände artenreicher Auenwiesen im Untersuchungsgebiet zu finden. Zu dieser Zeit starteten auch erste großflächige Renaturierungsmaßnahmen, in deren Zuge mehrere hundert Hektar Ackerflächen in Grünland umgewandelt wurden. Als Renaturierungsmaßnahmen wurden diese Flächen entweder der Selbstbegrünung überlassen oder mit einer artenarmen gräserdominierten Grasmischung eingesät.

Zusätzliche Maßnahmen zur Artenanreicherung, wie die aktive Einbringung von Samen seltener Zielarten wurden nicht durchgeführt, da die Randbedingungen für eine erfolgreiche und selbstständige Wiederbesiedlung der Flächen durch Zielarten als sehr günstig eingeschätzt wurden. Diese Einschätzung beruhte zum einen auf der Annahme, dass die Zielarten sich aus der Samenbank wiederetablieren würden und zum anderen auf der Erwartung, dass eine Wiederbesiedlung von Restpopulationen der Zielarten im unmittelbaren Umfeld der umgewandelten Flächen ausgehen würde.

Das Ergebnis dieses Wiederbesiedlungsprozesses unter Berücksichtung der vorherrschenden Standortbedingungen wurden in einem Naturschutzgebiet, zehn Jahre nach Unterschutzstellung und Umwandlung der eingeschlossenen Ackerflächen in Grünland untersucht (Kapitel 5). Die Untersuchungen wurden in dem relativ kleinen (75ha), durch Gräben und Wege reich strukturierten Naturschutzgebiet „Riedwiesen von Wächterstadt“ durchgeführt. Das Gebiet umfasst neben Neuwiesen, die Ende der achtziger Jahre des letzten Jahrhunderts angelegt wurden, auch Altwiesen, die stets als Grünland bewirtschaftet wurden. Restpopulationen von Zielarten sind entlang von Gräben und Wegen und in Altwiesen zu finden. Neuetablierte Populationen in Neuwiesen sind aufgrund der ackerbaulichen

Vornutzung eindeutig zu identifizieren. Während die Analyse der Standortbedingungen und der erhobenen Vegetationsaufnahmen nur geringe Unterschiede bezüglich der vorherrschenden Standortfaktoren (z. B. Nährstoffversorgung) zwischen Alt- und Neuwiesen zeigte, traten deutliche Unterschiede in der floristischen Komposition der zwei Wiesentypen auf. Die Vegetation der Neuwiesen war entlang vorherrschender Gradienten der Umweltvariablen (z. B. Feuchtegradient) weniger ausdifferenziert als dies in den Altwiesen der Fall war. Dementsprechend waren unterschiedliche Artengruppen typisch für die zwei Wiesentypen, Indikatorarten der Altwiesen waren vor allem ausdauernde Hemikryptophyten, häufig mit überwiegend vegetativer Ausbreitung, während in Neuwiesen Arten ruderaler, regelmäßig gestörter Standorte überwogen, welche darüber hinaus auch meist in der Lage sind eine persistente Bodensamenbank aufzubauen.

Trotz günstiger Rahmenbedingungen für die Wiederbesiedlung der neuen Grünlandflächen (d. h. geringe Biomasseproduktion, geringe Deckung, relativ geringe Nährstoffversorgung) fand eine Wiederbesiedlung nur in sehr geringem Maße statt und beschränkte sich fast ausschließlich auf die unmittelbare Umgebung der Restpopulationen entlang der Gräben und Wege. Dies zeigte sich auch in der punktgenauen Kartierung der Vorkommen von 23 Zielarten. Selbst bei windverbreiteten Arten war die überwiegende Mehrheit der seit der Umwandlung der Flächen in Grünland neuetablierten Individuen in unmittelbarer Nähe der Restbestände anzutreffen. Neben der geringen Bedeutung der Samenbank für die Re-etablierung von Zielarten, fanden sich auch keine Anzeichen, dass regelmäßige Überflutung, Heuwerbung oder Nachbeweidung im Herbst einen positiven Einfluß auf die Wiederbesiedlung der Neuwiesen hatte. Selbst unter den im Untersuchungsgebiet vorgefundenen günstigen Rahmenbedingungen für die Wiederbesiedelung neuangelegter Grünlandflächen zeigte sich, dass die Re-etablierung typischer Auenwiesenbestände stark durch die Ausbreitungsfähigkeit der Zielarten limitiert wird.

Während in Kapitel 5 der mögliche Beitrag der Bodensamenbank für die Wiederansiedlung typischer Arten und Vegetation der Auenwiesen nur indirekt erfasst werden konnte, wurde dieser in der in Kapitel 6 dargestellten Studie direkt bestimmt. Dazu wurde die aktuelle Samenbank auf tiefliegenden Ackerflächen in der Altaue erfasst, welche in der Vergangenheit Wuchsorte artenreicher Auenwiesen waren. Die Studie wurde nach einem langandauernden Frühjahrshochwasser des Rheins im Jahr 2001 durchgeführt, so dass auf den Untersuchungsflächen die Feldfrüchte abgestorben waren und an deren Stelle Artenkombinationen der Zwergbinsen und Zweizahnfluren (Klassen Isoëto-Nanojuncetea und

Bidentea) wuchsen. Sowohl in der oberirdischen Vegetation als auch in der Samenbank fanden sich keine Zielarten der Auengrünlandrenaturierung. Dominierend waren typische Schlammflur- und Ackerarten. Dies bestätigt, dass nach mehreren Jahren der Ackernutzung die Samenbank der Auenwiesengesellschaften zur Gänze aufgezehrt ist.

Im Gegensatz zur geringen Bedeutung der Samenbank für die Auengrünlandrenaturierung in Ackerflächen zeigte sie eine hohe Bedeutung für die Erhaltung einer anderen bedrohten Vegetationseinheit, der ephemeren Schlammflurvegetation. Die Studie zeigt, dass unregelmäßig überflutete Ackerflächen wichtige Sekundärhabitate für Arten der Schlammfluren, die ihre Primärhabitate im Schwankungsbereich unterhalb der Mittelwasserlinie von Flüssen besitzen, darstellen. Da sich die Artengemeinschaft an ihren Sekundärstandorten nur alle 3 bis 4 Jahre ausbilden kann ist sie dort gefährdet durch Bewirtschaftungsregimes, welche die regenerative Reproduktion verhindern, aber auch durch verbesserte Drainage oder das Verfüllen von Senken.

Wenn eine Besiedlung ehemaliger Ackerflächen oder artenverarmter Grünlandbestände von Restbeständen typischer Auengrünlandarten oder der Samenbank nur in geringem Maße bzw. nicht stattfindet, ist es notwendig die Ausbreitungslimitierung der Arten durch den aktiven Übertrag von Samen der Zielarten, z. B. durch Mahdgutübertrag, zu überwinden. In Kapitel 7 sind Untersuchungen zu den Auswirkungen möglicher Behandlungsvarianten, die mit einer solchen aktiven Einführung von Samen einhergehen, dargestellt. Untersucht wurden die Effekte einer Störung der vorhandenen Grasnarbe, der Auftrag von Streu, wie dies auch im Rahmen von Renaturierungsmaßnahmen geschieht, als auch die Anwendung einer simultanen Graseinsaat bei der Einbringung von Samen der Zielarten. Letzteres ist von besonderer Bedeutung, unter dem Gesichtspunkt der Integration von wiederhergestellten Auenwiesen in die landwirtschaftliche Nutzung. Dazu wurde der Effekt von zeitgleich mit Zielarten gesäten Gräsern auf das Auflaufen, die Überlebensrate und die Phase der frühen Etablierung von 6 typischen Pflanzenarten der Auenwiesen am hessischen Oberrhein (*Arabis nemorensis*, *Iris spuria*, *Serratula tinctoria*, *Silaum silaus*, *Pseudolysimachion longifolium*, *Viola pumila*) im Rahmen von zwei Feldexperimenten in der Alt- und Rezentaue untersucht. Der Einfluß von Störung und Streu auf das Auflaufen, die Überlebensrate und die Phase der frühen Etablierung der gleichen Arten wurde in einem Experiment in der Rezentaue untersucht.

Die meisten Arten reagierten bezüglich Auflaufen, Überlebensrate und Etablierung, wie erwartet, positiv auf die Störung der Grasnarbe und negativ auf den Auftrag von Streu. Die gleichzeitige Einsaat von Gräsern zeigte keinen einheitlichen Effekt, allerdings ergab sich auf

Artebene in den meisten Fällen eine höhere Überlebens- und Etablierungsrate bei gleichzeitig ausgesäten Gräsern. Diese positive Reaktion der Individuen der Zielarten könnte auf einen Schutzeffekt der umgebenden Gräser während des ausgesprochen trockenen Sommers im Jahr 2003 zurückzuführen sein. Wesentlich deutlicher als die Effekte der unterschiedlichen Behandlungsvarianten waren die Unterschiede zwischen der Alt- und Rezentaue. Während die Auflaufraten sich in beiden Auenkompartimenten kaum unterscheiden, waren in der Altaue aufgrund des dort herrschenden stabileren Grundwasserstandes sowohl die Überlebensraten als auch die Etablierungsraten deutlich höher.

Die Ergebnisse bestätigen, dass sich die ausgebrachten Arten unter vielfältigen Bedingungen etablieren konnten, was den Schluss zulässt, dass auch im Fall von seltenen Arten nicht Standortfaktoren, sondern die Ausbreitungslimitierung der wesentliche Faktor für die gegenwärtig vorzufindenden Vegetationsmuster in den Auenwiesen ist. Die Tatsache, dass gleichzeitig eingesäte Gräser im Gegensatz zu einer vorhandenen dichten Grasnarbe die Etablierung der Zielarten nicht beeinträchtigten, eröffnet die Möglichkeit, die divergierenden Interessen von Landwirten und Naturschützern in Projekten zur Grünlandrenaturierung leichter in Übereinstimmung zu bringen. Damit scheint es möglich, die Integration der neuangelegten Auenwiesenbestände in die landwirtschaftliche Nutzung zu beschleunigen und somit den Erhalt der Auenwiesen langfristig zu sichern.

Allerdings ist eine landwirtschaftliche Nutzung nur dann sicherzustellen, wenn sowohl die Quantität als auch Qualität der Aufwüchse dies zulässt. Dazu wurden Unterschiede in der Qualität und Quantität der Aufwüchse bezüglich Vegetationstyp, Standortbedingungen, Bewirtschaftungsgeschichte, Artenreichtum und Naturschutzwert untersucht. In die Studie eingeschlossen waren die flächenmäßig bedeutendsten Auenwiesentypen im Bereich des hessischen Oberrheins. Dies sind Grünlandbestände der Verbände *Arrhenatherion*, *Cnidion*, *Magnocaricion*, welche einen Gradienten zunehmender Überflutungshäufigkeit widerspiegeln.

Dieser Gradient in der Überflutungshäufigkeit sowie Unterschiede in der Artzusammensetzung und Naturschutzwertigkeit führten zu einer klaren Aufgliederung der Vegetationsaufnahmen in einer „Detrended Correspondence Analysis“. Im Gegensatz zu diesen deutlichen floristischen Unterschieden konnten nur geringe Unterschiede bezüglich Aufwuchsmenge und -qualität zwischen den einzelnen Zustandsklassen gefunden werden, insbesondere in den *Arrhenatherion*-Gesellschaften der trockeneren Standorte. Dagegen zeigte sich in den *Cnidion*-Gesellschaften, dass sowohl Aufwuchsmenge als auch -qualität bei höherer Naturschutzwertigkeit der Flächen erhöht waren. Dies ist vermutlich auf eine

Verschiebung der Anteile der funktionalen Gruppen zurückzuführen, z. B. auf einen Anstieg des Kräuteranteils. Dementsprechend konnte die in der jüngeren Vergangenheit in Experimenten aufgestellte Hypothese welche eine generelle Zunahme der Produktivität allein auf zunehmende Artenvielfalt zurückführte nicht bestätigt werden.

Darüber hinaus lässt sich aber feststellen, dass artenreiche Auengrünlandbestände wie sie am hessischen Oberrhein anzutreffen sind bzw. in Renaturierungsprojekten wieder angelegt werden gut für landwirtschaftliche Futtergewinnung genutzt werden können. In Phasen mit erhöhtem Nährstoffbedarf der Tiere, wie Trächtigkeit oder Laktation wird bei Verwendung des gewonnenen Heus als Grundfutter Zufütterung nötig sein.

Aufgrund der guten Möglichkeiten die Grünlandbestände in landwirtschaftliche Nutzung zu integrieren, erscheinen die Bedingungen für eine nachhaltige Entwicklung und Sicherung von artenreichem Auengrünland am hessischen Oberrhein sehr günstig. Die fehlende oder sehr geringe Verfügbarkeit der Diasporen von Zielarten aus der Samenbank oder durch Eintrag von außerhalb muss hierbei aber durch aktive Einbringung überwunden werden. Die große Variabilität der Auswirkungen verschiedener Behandlungsvarianten, die im Rahmen solcher Maßnahmen angewendet werden, legt nahe, dass es sinnvoll ist die Ausbringung von samenhaltigem Mahdgut auf einer Renaturierungsfläche zeitlich und räumlich versetzt zu wiederholen.

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Erklärung

Ich erkläre: Ich habe die vorgelegte Dissertation selbständig und ohne unerlaubte fremde Hilfe und nur mit den Hilfen angefertigt, die ich in der Dissertation angeben habe.
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