Applied Vegetation Science 6: 13-22, 2003
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The impact of site conditions and seed dispersal on restoration success in alluvial meadows

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Abstract. We studied the restoration success of flood plain meadows in the northern Upper Rhine valley, where between 1988 and 1992, 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 phytosociological 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 recolonization 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.

Nomenclature: Wisskirchen & Haeupler (1998).

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 fail to re-establish, even after the soil nutrient status and the biomass production have been successfully adapted (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 1996; 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 ca. 20 yr (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 yr 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 extensively 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 hay-making from June onwards (Strykstra et al. 1997) as well as by aftermath grazing with a large migratory flock of sheep (Gibson et al. 1987; Fischer et al. 1996), with the latter possibly enhancing establishment (Gibson et al. 1987). More than 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, we compared, in 1999, 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 not under arable use, while new meadows, prior to their conversion, were used at least for 20 yr. 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?

Material and Methods

Study site

The study area is situated in the Hessian portion of the Holocene flood plain of the River Rhine ca. 30 km southwest of Frankfurt, Germany (49°51' N, 8°23' E; 85 m a.s.l.). It comprises a nature reserve of 75 ha (Fig. 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 flooding, 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, very 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 northwestern limits of their distribution areas (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 fertilizer and mowing 2 to 3 × 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 (*Arrhenatherum elatius*, *Festuca pratensis*, *F. 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 fertilizer 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 recolonization.

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 m × 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). 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 hr 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 a CN-Analyzer (Flash EA 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 to 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 recolonization of the ex-arable land by plants in greater detail, we mapped the populations of 23 target species (as listed in Fig. 2) with precision. 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, nitrogen and soil-reaction (Ellenberg et al. 1991). Correlations between environmental variables were analysed with the 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 (75 out of 116). 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 of McCune & Mefford (1999a). Correlations between a subset of site and vegetation parameters and the DCA sample scores were analysed with 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 recolonization 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 recolonization of new meadows. In the second model, variables were log-transformed prior to data analysis for normalization. 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 1999b).

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			Bonferroni-Holm
	x	*sem*	*x*	*sem*	*P*	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	0.1	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)	729.1	32.4	588.7	23.7	0.003 *	0.008
C/N ratio	10.6	0.09	10.3	0.08	0.012	0.01
Species number	23.6	1.21	26.9	1.18	0.066	0.013
Ellenberg reaction value	6.9	0.05	6.9	0.1	0.163	0.017
Ellenberg nitrogen 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

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.

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.

The DCA ordination had a total inertia of 1.878. The first axis had the highest eigenvalue (0.40), while the eigenvalues of axes 2 and 3 (0.13 and 0.08) indicated their minor importance. The gradient lengths of axes 1 and 2 both exceeded 2 sdu (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 axes 2 and 3 contributed only ca. 0.05 each.

The DCA ordination plot (Fig. 1a) displayed a clear separation of old and new meadows along axes 1 and 2. New meadows were much more aggregated in ordination space, while old meadows showed a much wider scatter.

The first DCA axis displayed a strong correlation with the environmental variables age, P, K and 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 Fig. 1a.

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	Nitrogen value	Reaction value	Phosphorus	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							
Nitrogen value	–0.21	–0.27	0.20	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*

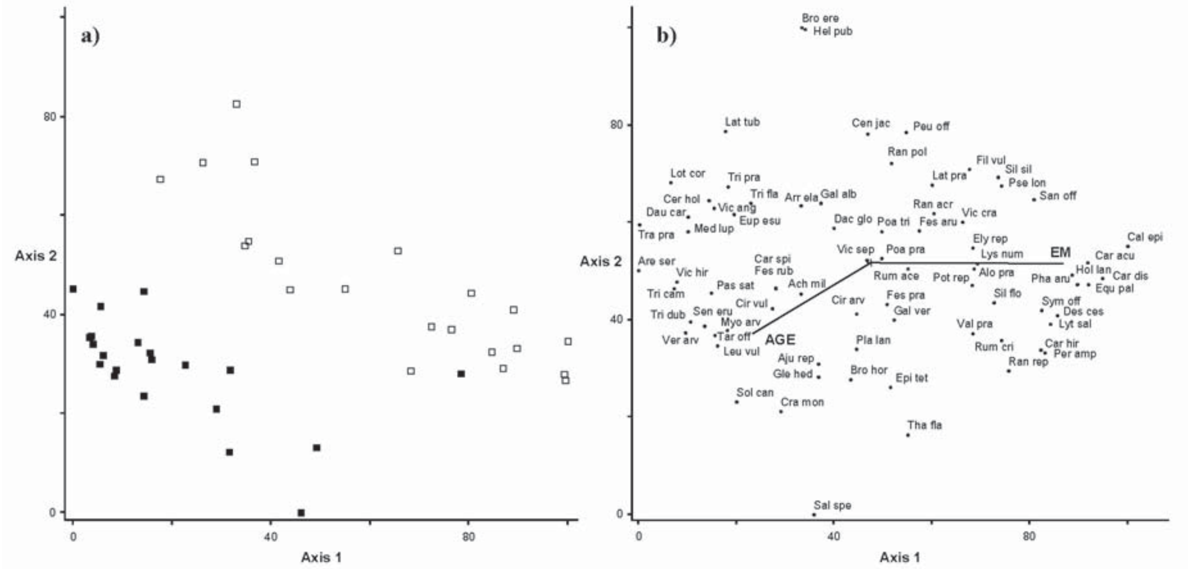

Fig. 1. DCA ordination diagrams. **a.** Scores of all relevés along axes 1 and 2. Filled squares represent new meadow- and empty squares old meadow relevés. **b.** Joint plot (axes 1 and 2) of DCA scores of all species with more than two occurrences and the vectors of age (old = 0; new = 1) and the Ellenberg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

Table 4 shows the species typical of old and new meadows with a significant indicator value of at least 25 according to the method of Dufrêne & 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 (Fig. 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 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.

Table 3. Spearman rank correlation coefficients between sample scores on the first two DCA axes of the full data set ($N = 42$), site and vegetation variables. * ≤ 0.05, ** ≤ 0.01, *** ≤ 0.001. Coefficients ≥ 0.5 in bold.

	Axis 1		Axis 2	
Age	**–0.72**	***	**–0.52**	***
Phosphorus	0.47	**	0.23	
Potassium	**–0.67**	***	–0.01	
C/N ratio	0.14		0.14	
Moisture value	**0.82**	***	–0.09	

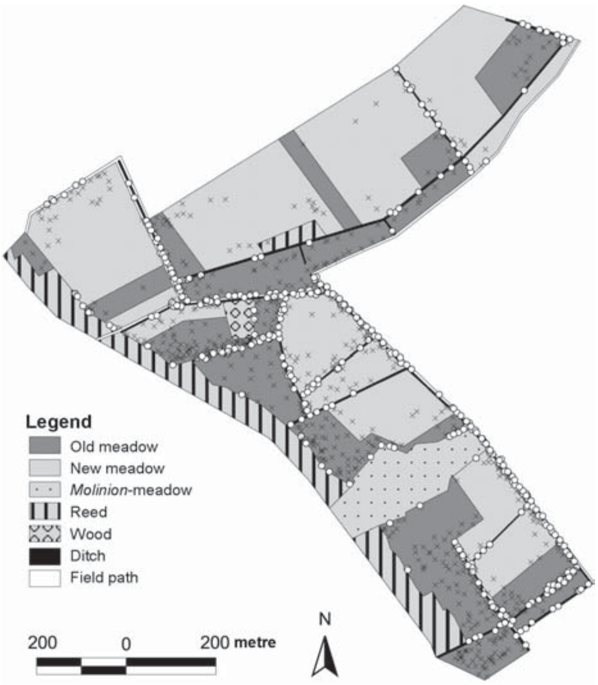

Fig. 2. Distribution of target species in the study area. Individuals/subpopulations of target species along ditches are identified by circles, in meadows by crosses. List of the target species with number of occurrences in brackets:

Allium angulosum (18), *Arabis nemorensis* (7), *Carex praecox* (59), *Carex tomentosa* (78), *Cirsium tuberosum* (87), *Cnidium dubium* (1), *Dianthus superbus* (1), *Euphorbia palustris* (27), *Filipendula 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 4. Indicator Species of old and new meadows. Significance obtained by the Monte-Carlo-Permutations Test: * ≤0.05, **≤ 0.01, ***≤ 0.001. ° = wind-dispersed (seeds with pappi). IV = Indicator Value (%); 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 weed in the study area; ( ) = not indicated.

	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 cracca	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	**	( )	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	***	( )	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 hordeaceus	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

For three species, the minimum range of dispersal and establishment over the last 10 yr is given in Fig. 3. Dispersal was analysed in areas where the occurrences in new meadows were clearly linked to source populations along adjacent ditches. The wind-dispersed *Cirsium 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 yr, while the values of *Carex tomentosa* and *Peucedanum officinale* were much lower with 1 and 4 m, respectively.

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, Nt 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 nitrogen 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

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 = P-value of the global F-test for the deviation of the parameter estimates from zero.

	Parameter estimate	P	R^2	ANOVA 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					

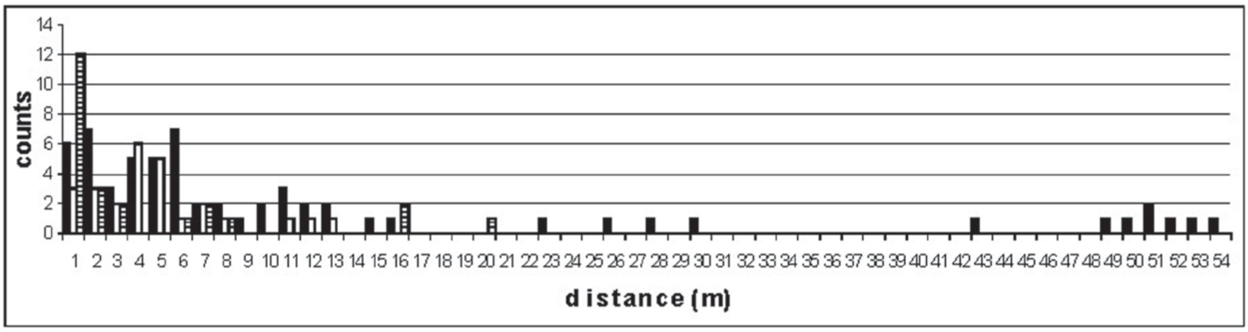

Fig. 3. Minimum dispersal and establishment distances of *Cirsium tuberosum* (black), *Peucedanum officinale* (white) and *Carex tomentosa* (hatched) since 1992. The number of individuals of each species in new meadows is plotted against their distance to the closest ditch with occurrence of the respective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

fertilizer 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.

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 agrestal species which, in our case, are of no conservational interest. However, target species are still found in higher numbers and abundance in old meadows (Fig. 2).

These floristic differences reappear in the DCA plot, revealing a clear and strong differentiation between new and old meadows (Fig. 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 greater 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 characterized 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 (Fig. 1b). In contrast, a great number of ruderals and weeds were still characteristic of new meadows. As a rule, indicator species 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 the DCA ordina-

Table 6. Nutrient content classes used in agricultural grassland management for plant available P and K (mg/100 g) in meadows; capital letters indicate the degree of fertilization needed to sustain mean biomass yields: A = strongly raised fertilization; B = slightly raised fertilization; C = moderate fertilization to sustain productivity; D = reduced fertilization; E = no fertilization (Anon. 1993).

	A	B	C	D	E
P	0-2.7	2.8-6.3	6.4-11.2	11.3-17.3	17.4 -
K	0-5.3	5.4-12.0	12.1-21.3	21.4 -32.8	32.9 -

tion. None of these species have special adaptations for wind-dispersal, and most of them have been categorized as species with transient or short-term persistent seed bank (Thompson et al. 1997). Both traits are regarded as important characteristics for re-establishment. In contrast, indicator species 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 the 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 (Fig. 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 with 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 for 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. Small and fragmented remnant populations in such sites, notably along 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).

A densely closed canopy structure may be another limiting factor in grassland restoration. While annuals and other short lived ruderals dominating early successional stages are usually not hampering the re-establishment 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 & Lepš 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 not rapidly accepted 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 10 yr. Traditional agricultural dispersal processes, such as hay-making 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.

Acknowledgements. We thank Astrid Dempfle for her help in taking the soil samples, collecting the relevés and mapping of the target species, Josef Scholz-vom Hofe for his support in soil nutrient analyses, Lutz Eckstein and Michael Ashdown for reading the manuscript. We also thank the coordinating editor Rob Marrs and two anonymous reviewers for helpful comments on a former version of this paper. The research was partially funded by the German Federal Agency for Nature Conservation (BfN).

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Received 6 July 2002;
Revision received 2 November 2002;
Accepted 22 November 2002.
Coordinating Editor: R.H. Marrs.

For App. 1, see JVS/AVS Electronic Archives;
www.opuluspress.se/pub/archives/index.htm