Dispersal and establishment of floodplain grassland species as limiting factors in restoration

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Received 22 August 2000; received in revised form 14 May 2001; accepted 29 May 2001

Abstract
The restoration of grassland and its dependence on the dispersal of characteristic plant species was analysed in the Saale River floodplain near Halle (Germany). Species composition and soil nutrient content were investigated in grassland converted to extensive management in 1989 (“restoration grassland”) and in adjacent grassland that had never been managed intensively (“old grassland”). In two experiments dispersal of *Silaum silaus* and *Serratula tinctoria* was studied following introduction of these species into “restoration grassland”. Seeding establishment was recorded and compared with the “old grassland”. Ten years after conversion to extensive management, characteristic floodplain grassland species had only reappeared in locations very close to “old grassland”. There were still differences in soil nutrient content of both grassland sites but a comparison of seedling survival provided evidence that conditions of establishment were similar. However, establishment rates appeared to be low in both grassland types indicating that a large initial input of seeds is required for re-establishment. Seeds of *Silaum silaus* and *Serratula tinctoria* were dispersed very short distances. About 75% of the seedlings were found within 1.5 m of parent plants. Management and flooding did not increase dispersal distances. The results strongly suggest that poor dispersal was the main limiting factor in determining the success of restoration. The implications of this result for nature conservation are discussed. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Grassland restoration; Re-establishment; Dispersal distances; *Silaum silaus*; *Serratula tinctoria*

1. Introduction
In the last 50 years, widespread losses and ecological degradation of European wet grasslands have occurred (Joyce and Wade, 1998). This has been largely due to agricultural intensification including land drainage, application of inorganic fertilizers and other agrochemicals, and the conversion of permanent grassland to arable crops (Fuller, 1987; Hundt, 1996). In the 1970s, several projects were started to restore historically species-rich grassland plant communities (Bakker, 1989). Since 1992 all nations of the EU have supported the change to extensive grassland management through various financial compensation mechanisms (EU-Directive No. 2078/92). However, restoration and extensification programmes have not always been successful in re-establishing formerly typical grassland species. In many cases, characteristic species have not reappeared even several years after cessation of intensive agriculture (Graham and Hutchings, 1988; Bakker, 1989; Kapfer, 1994). There are two factors that may hamper re-establishment:

1. Site limitation: the site conditions (management inclusive) are inappropriate.
2. Dispersal limitation: no seeds or other propagules are available

Early studies on grassland restoration have concentrated on site limitation. It is well known now that the depletion of fertilizer residues requires much time and that floristic recovery is hampered by a high nutrient supply (Gough and Marrs, 1990; Berendse et al., 1992; Tallowin et al., 1998). However, recreating appropriate abiotic site conditions alone is often not sufficient in restoring species-rich grassland communities (Berendse et al., 1992; Kapfer, 1994). Authors of recent papers have pointed out that the availability of propagules can be a serious bottleneck in grassland
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restoration (Bakker et al., 1996; Strykstra et al., 1998). The seed bank of many grassland species is only transi-ent or of short-term persistence and cannot survive longer periods of intensive management (McDonald et al., 1996). Therefore, an input of seeds or other propagules from outside is often necessary to re-establish populations. The probability of such inputs depends (1) on the distance to source populations and (2) on disper-sal properties of the species. In the present agricul-tural landscape of central and western Europe, such semi-natural habitats as extensive grasslands are often fragmented and seed sources may be far away from restoration sites (Peschlod et al., 1996).

Our knowledge about dispersal properties of grass-land species, particularly about dispersal distances, is very limited. The results of some studies indicate that agricultural practices such as mowing (Strykstra et al., 1997) and grazing (Fischer et al., 1996) enhance disper-sal processes in grasslands. However, for the major-ity of grassland species the efficiency of different dispersal vectors and processes is totally unknown.

In this paper, the relationship between dispersal and restoration process was analysed in grassland of the Saale River floodplain. The floodplain comprises “restoration grassland” which was converted to extensive management in 1989 and “old grassland” which has never been managed intensively. The “restoration grassland” was ploughed in the 1970s and 1980s to grow arable crops or forage grasses and inorganic ferti-lizer was applied (Kompa et al., 1999). Since 1989 these fields have been managed in the same way as the “old grassland”, i.e. by grazing and cutting without any fer-tilizer application. Ten years later, many characteristic species that were abundant in “old grassland” had not reappeared at the restoration sites.

The study focused on whether conditions of estab-lishment were less favourable in “restoration grassland” than in “old grassland” or whether re-colonization was limited by dispersal. Dispersal and establishment of two characteristic species, Serratula tinctoria and Silaum silaus, were analysed following introduction into restoration grassland.

2. Material and methods

2.1. Study sites

Apart from dispersal experiment 1 (see Section 2.3.), all studies were performed in the Saale River floodplain near Holleben, 10 km south of Halle (Germany). The floodplain is located west of the river and is about 1 km wide. An old ditch system drains the grassland. There is no artificial dam between river and floodplain but the height of the river bank is about 1 m above the average floodplain level. Therefore, flooding reaches the study area through the ditches or by rise in groundwater level. Inundation is common in winter and spring but does not occur every year. In the research period (1998–2000) all study sites of the floodplain were flooded three times for a total of 120 days. To exclude differences in hydro-logical conditions all study sites were positioned in areas of the same height (0.8 m above average river level). Since rainfall is quite low (490 mm/year), site conditions are characterized by large fluctuations in soil moisture. The soil consists of heavy alluvial clay (1.5–2.5 m) and pH-values are about 7.3 (0.1 n KCl).

The management has been extensive in all parts of the study area since 1989. Usually, the grass is cut at the beginning of June and grazed by cattle in September or October. Sometimes aftermath grazing is replaced by a second cut. In the 1970s and 1980s, parts of the flood-plain were selected for experiments to establish a more intensive way of grassland management or arable use. After the political change in Eastern Germany in 1989, intensive land use on such sites was no longer profitable. Nowadays, the grassland converted to extensive manage-ment (“restoration grassland”) is located adjacent to species-rich “old grassland” which reflects the potential grassland community. This community is characterized by species such as Silaum silaus, Serratula tinctoria, Sanguisorba officinalis, Allium angulosum and Thalic-trum flavum which have become rare in recent decades and are listed as endangered in the Red Data Book of the state (Saxonia-Anhalt).

2.2. Analysis of vegetation and site conditions

2.2.1. Transect plots

Five transect plots (10 m×55 m) were positioned in areas where “restoration grassland” was located adja-cent to “old grassland”. Plots were divided into 14 seg-ments as shown in Fig. 1. In each segment percentage cover of all species was estimated twice a year. To determine the soil seed bank composition, four soil samples per segment were taken in 1998, each of 3.7 cm in diameter and 10 cm in depth. Sampling date was in April, just before seedlings of the characteristic species emerged. Two of the samples were mixed to provide two composite samples per segment. They were placed on a thin layer of sand in plastic boxes which were protected by transparent lids against seed rain. The plastic boxes were exposed in a cold frame within 2 days after sam-ping. Seedling emergence was recorded twice a month until October 1999.

To analyse soil nutrient content, four soil samples were taken from the “old grassland” segment (−5 to 0 m) and from the furthest “restoration grassland” seg-ment (45 to 50 m) of each transect plot. Samples were separated into topsoil (0–15 cm) and a deeper soil layer (15–30 cm). To measure mineral nitrogen content (N\(_{\text{min}}\)) fresh samples were sieved (4 mm) and extracted with
potassium sulphate. Transmission of the extracts was measured photometrically (EPOS-Eppendorf, Inc.). For analysis of total nitrogen (N_t), total carbon (C_t), plant available potassium (K) and phosphorous (P), the samples were dried and ground. N_t and C_t were determined by the element analyser “vario el” (Elementar, Inc.). P and K were analysed by ICP–AES following extraction in a calcium lactate solution. Undisturbed soil samples were dried and weighed to analyse bulk density. The mean groundwater level, which was monitored monthly by one dipwell in each transect plot (2 m long auger holes lined by permeable plastic tubes), was 0.29 m below the surface. The level ranged from a maximum of 0.73 m above (November 1998) to a minimum of 0.98 m below the surface.

2.2.2. Distant plots
To study the effect of the distance to “old grassland”, the same analyses were performed on a further 15 plots (10×10 m) of “restoration grassland” located >500 m away (Fig. 1). These plots were grouped together in three complexes of five plots each. Vegetation analysis, soil nutrient content and groundwater levels were determined using the methodology described earlier. Vegetation analysis was performed in each plot, soil variables (four samples/complex) and groundwater level (one dipwell/complex) were examined in each complex. The average groundwater level was 0.38 m below the surface (max.: +0.63 m, min.: −1.05 m).

2.3. Experiments on dispersal
Two experiments were carried out to analyse the dispersal capacity of two species, *Silaum silaus* and *Serratula tinctoria*, which were common in “old grassland” but extremely rare in “restoration grassland”. In both experiments, areas were selected in which the species were previously absent. *Silaum silaus* is a perennial Apiaceae with annual shoots (Bischoff, 2000). The seeds have no morphological adaptations to wind or water dispersal, but anemochory and transport by running water are described as dispersal mechanisms (Müller-Schneider, 1986). *Serratula tinctoria* is a perennial Asteraceae. The flowering shoots are annual, but a part of the vegetative shoots or rosettes survive the winter. The seeds have a pappus which enables wind and water dispersal. Epizoochorous transport by animals is also described (Müller-Schneider, 1986).

Experiment 1 was started in an unmanaged field outside the floodplain to exclude the effect of management and flooding (Fig. 1). The distance to the nearest populations was >5 km. Sixty parent plants of each species were collected in “old grassland” and transplanted to four places (15/planting site) of the unmanaged field in early September when seeds were almost ripe. Since species composition and vegetation structure were different to the floodplain, and to simplify the following detection of seedlings, vegetation was entirely removed in an area of 5 m radius around the parent plants. Afterwards the planting sites were left undisturbed. To estimate total seed number per planting site, secondary umbels of *Silaum silaus* and flower heads of *Serratula tinctoria* were counted and the mean seed number of 20 secondary umbels and flower heads was assessed. Samples of seeds (5×50 of each species) were placed on moist filter paper in Petri dishes to examine germinability (20/10 °C with a day/night period of 13/11 h, stratification: 2 month, 5 °C). In the following year, the position of all *Silaum silaus* and *Serratula tinctoria* seedlings which emerged within a distance of 5 m around the parent plants was recorded.

Experiment 2 was performed in “restoration grassland” using the same approach as in experiment 1 (Fig. 1). Again 60 parent plants with almost ripe seeds were transplanted to four places (15/planting site), but unlike experiment 1, the planting sites were managed by grazing and cutting. To avoid an undesirable external seed input the four plantings were placed at a distance of >200 m from each other and from other populations of the two species. Almost all introduced plants were eaten by cattle from late September to early October.
Since it was not clear if *Silaum silaus* and *Serratula tinctoria* could be dispersed endozoochorically, the planting was repeated in the middle of October. The parent plants had to be taken from another area because the source populations of the first planting had also been grazed at that time. The investigation of seed production and germinability followed experiment 1. To obtain information about the dispersal phenology, 50 seed traps (funnel traps, \( \Omega = 10 \) cm) were positioned in five concentric circles at a distance of 1–5 m from each planting (Fig. 1). The traps were emptied and checked for seeds of *Silaum silaus* and *Serratula tinctoria* in September (before grazing), October (after grazing), December (after 1st inundation) and April (after 2nd inundation). To analyse dispersal distances and direction, the seedling emergence was recorded in 50 quadrats (0.5 x 0.5 m) per planting placed next to each trap. In the central circle (0.5 m) all seedlings were counted.

To obtain information about endozoochorous dispersal, the 25 dung pats nearest to each planting site were marked after grazing in October. The emergence of *Silaum silaus* and *Serratula tinctoria* seedlings within the dung pats was examined in May of the following year. After both inundations a 50 m line of drift material was clearly visible between 100 m (nearest) and 500 m (furthest) east to north-east of the plantings. The height of this part of the river bank was greater than the maximum flooding level. In the following spring, seedling emergence was recorded in the entire drift line.

2.4. Analysis of seedling survival

To compare conditions of establishment, seedling survival of *Silaum silaus* and *Serratula tinctoria* was analysed in “restoration” and “old grassland”. In May 1999, 10 seedlings (cotyledon stage) were marked with plastic rings and cocktail sticks around the planting sites of “restoration grassland” \( (n = 4) \), and likewise five seedlings in the “old grassland” part of each transect plot \( (n = 5) \). Seedlings of *Serratula tinctoria* were only found in four transect plots. Developmental stage and survival were recorded every 3 to 4 weeks.

2.5. Statistics

The effect of the distance to the edge of “old grassland” on the cover sum of characteristic species (see Section 2.1.) in “restoration grassland” was tested by ANCOVA with “transect” as factor and “distance” as covariable. To comply with the assumptions of homogeneity of variances, unimodal distribution and linearity between covariable and variable, cover values were arcsine \( \sqrt{x} \) transformed and distance values were log \( (x + 1) \) transformed. To compare soil characteristics the mean values of the four samples from each transect segment (Section 2.2.1.) and distant plot (Section 2.2.2.) were calculated for further analysis. Differences within the transect plots (“old grassland” segments versus “restoration grassland” segments) were analysed by a \( t \)-test for paired samples. The distant plots and the “old grassland” segments of the transect plots were compared by a \( t \)-test for independent samples. The spatial distribution of seedlings around the parent plants (mean values of four sites) was analysed by a chi-square test (H0: distribution uniform). Using GLIM (binomial errors, logit link function, Crawley, 1993), differences in raw proportion data of seedling survival were analysed by a generalized linear model. Since the residual deviance was larger than the residual degrees of freedom (overdispersion) the resulting scaled deviances were compared by an \( F \)-test instead of chi-square.

3. Results

3.1. Vegetation and site conditions

Ten years after cessation of intensive management, characteristic floodplain grassland species were still rare in “restoration grassland” (Fig. 2). The relationship between the occurrence of these characteristic species and the distance to “old grassland” was highly significant. Their cover sum decreased from 13% in “old grassland” to 3.5% at a distance of 6 m down to 1% beyond 10 m. Even the abundance of *Serratula tinctoria* and *Silaum silaus*, which were common in “old grassland” (cover 11.2%) was very low in “restoration grassland” (mean cover <1%). In the ANCOVA, the transect effect and the interaction between transect and distance were also significant. This result indicated that the transect plots were different in the average cover value of characteristic species and in the slopes of the...
cover–distance curves. However, the largest proportion of variability was explained by the covariable distance. In the 15 “distant plots” (> 500 m from “old grassland”) only *Serratula tinctoria* (two individuals) was found.

No characteristic species were found in the soil seed bank of “restoration grassland”. However, seeds of these species were also extremely rare in the soil of “old grassland” even where they were abundant in above-ground vegetation; altogether, only two seeds of *Silaum silaus* and one of *Serratula tinctoria* were recorded.

The analysis of nutrients in the topsoil showed that the content of C<sub>t</sub>, N<sub>t</sub> and N<sub>min</sub> was higher in “old grassland”, both in comparison with “restoration grassland” in the transect plots and “distant plots” of “restoration grassland” (Table 1). In the deeper soil layer no differences in these values were found. “Restoration grassland” (transect segments and distant plots) contained more plant available phosphorus in the deeper soil layer but not in the topsoil. Plant available potassium was higher in both layers of this grassland type. The differences in bulk density were small and not significant.

### 3.2. Dispersal experiments

In experiment 1, parent plants of *Silaum silaus* produced ca. 5864 seeds per planting site which was estimated from the number of umbels. The germinability of seeds determined in Petri dishes was 66%. In the field, an average of 183 seedlings per planting site emerged (i.e. 3.1% of seeds produced by parent plants). Seventy-three percent of the seedlings were found within a distance of 1.5 m and only 0.9% of the seeds were dispersed beyond 3.5 m although the recording area increased (Table 2). The average seed production of *Serratula tinctoria* parent plants calculated from the number of flower heads, was 3068 per planting site. Eighteen percent of the seeds germinated in Petri dishes and only six seedlings per planting site emerged in the field (i.e. 0.2% of seed number produced by parent plants). Distribution of seedlings around the parent plants was similar to that of *Silaum silaus*.

In experiment 2, the seed production of *Silaum silaus* parent plants was ca. 47100, of which ca. 35 300 were introduced with the first and 11 700 with the second planting. Fifty-two percent of the seeds sampled from the first planting (before the plants were eaten by cattle) and 27% of seeds sampled from the second planting germinated in Petri dishes. Fourteen seeds per planting site were caught by the seed traps and 251 seedlings were recorded in the quadrats. Seed production of *Serratula tinctoria* parent plants was ca. 15 200 per planting site (1st planting 6700, 2nd planting 8500). Eight percent of the seeds germinated in Petri dishes. An average of 14 seeds was recorded in the seed traps and 219 seedlings in the quadrats.

### Table 1
Mean values of bulk density, total nitrogen and carbon, plant available nitrogen, phosphorous and potassium content in two soil layers

<table>
<thead>
<tr>
<th>Layer</th>
<th>Bulk density (g/cm&lt;sup&gt;3&lt;/sup&gt;)</th>
<th>N&lt;sub&gt;t&lt;/sub&gt; (%)</th>
<th>C&lt;sub&gt;t&lt;/sub&gt; (%)</th>
<th>N&lt;sub&gt;min&lt;/sub&gt; (mg/kg)</th>
<th>P (mg/kg)</th>
<th>K (mg/kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0–15 cm</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>OG (transect)</td>
<td>1.16</td>
<td>0.54</td>
<td>5.6</td>
<td>10.5</td>
<td>66.9</td>
<td>133.3</td>
</tr>
<tr>
<td>RG (transect)</td>
<td>1.25</td>
<td>0.40&lt;sup&gt;a&lt;/sup&gt;</td>
<td>4.1&lt;sup&gt;a&lt;/sup&gt;</td>
<td>5.3&lt;sup&gt;a&lt;/sup&gt;</td>
<td>58.6</td>
<td>170.1</td>
</tr>
<tr>
<td>RG (distant)</td>
<td>1.32</td>
<td>0.37&lt;sup&gt;b&lt;/sup&gt;</td>
<td>3.9&lt;sup&gt;b&lt;/sup&gt;</td>
<td>6.5&lt;sup&gt;b&lt;/sup&gt;</td>
<td>70.8</td>
<td>184.5&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>15–30 cm</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>OG (transect)</td>
<td>1.29</td>
<td>0.32</td>
<td>3.3</td>
<td>3.7</td>
<td>22.8</td>
<td>81.8</td>
</tr>
<tr>
<td>RG (transect)</td>
<td>1.23</td>
<td>0.33</td>
<td>3.5</td>
<td>3.3</td>
<td>43.8&lt;sup&gt;a&lt;/sup&gt;</td>
<td>113.6&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>RG (distant)</td>
<td>1.23</td>
<td>0.30</td>
<td>3.2</td>
<td>4.0</td>
<td>44.4&lt;sup&gt;b&lt;/sup&gt;</td>
<td>126.4&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<sup>a</sup> Significant difference (P < 0.05) between “old grassland” (OG) and “restoration grassland” (RG) of the transect plots, t-test for paired samples (n = 5, d.f. = 4)

<sup>b</sup> Significant difference between OG (n = 5) and the distant plots of RG (n = 3), t-test for independent samples (d.f. = 6)

### Table 2
Mean percentages of seedlings found at different distances from parent plants and their standard errors (in parentheses)<sup>a</sup>

<table>
<thead>
<tr>
<th>Distance (m)</th>
<th>Area (m&lt;sup&gt;2&lt;/sup&gt;)</th>
<th><em>Silaum silaus</em></th>
<th><em>Serratula tinctoria</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>No management</td>
<td>Usual management</td>
</tr>
<tr>
<td>0.0–0.5</td>
<td>0.8</td>
<td>26.6 (4.6)</td>
<td>22.9 (2.8)</td>
</tr>
<tr>
<td>0.6–1.5</td>
<td>6.3</td>
<td>46.6 (3.4)</td>
<td>51.5 (1.3)</td>
</tr>
<tr>
<td>1.6–2.5</td>
<td>12.6</td>
<td>18.9 (1.9)</td>
<td>17.5 (2.9)</td>
</tr>
<tr>
<td>2.6–3.5</td>
<td>18.8</td>
<td>7.1 (2.6)</td>
<td>5.4 (2.0)</td>
</tr>
<tr>
<td>3.6–4.5</td>
<td>25.1</td>
<td>0.9 (0.9)</td>
<td>2.1 (1.1)</td>
</tr>
</tbody>
</table>

<sup>a</sup> 100%: total number of seedlings between 0 and 4.5 m; n = 4.
In experiment 2 the dispersal distances of both species were very similar to experiment 1 (Table 2). Seventy-four percent of the *Silaum silaus* seedlings and 77% of the *Serratula tinctoria* seedlings were recorded within the nearest 1.5 m around the parent plants. Only 2 and 3% were found between 3.6 and 4.5 m although the area was 3.5 times larger than that between 0 and 1.5 m. Seedling densities decreased from 190 m⁻² underneath parent plants to about 1 m⁻² (*Silaum silaus 1.7, Serratula tinctoria 0.9*) at a distance of 3 m and to 0.3 m⁻² (*Silaum silaus 0.2, Serratula tinctoria 0.4*) at a distance of 5 m.

The spatial distribution of *Silaum silaus* and *Serratula tinctoria* seedlings around parent plants was nearly identical (Fig. 3). The hypothesis of a “uniform distribution of seedlings” was rejected by the chi-square test. A clear concentration was observed east and northeast of the parent plants. This corresponded with the prevailing wind direction which was west-south-west during the time of seed release (meteorological station of Bad Lauchstädt, 5 km from the study site).

A small proportion of seeds was already shed in September, before grazing (Fig. 4). Very few additional seeds were recorded in the traps until the second planting because cattle ate them together with those plants initially introduced. The majority of seeds was released between the second planting and the end of the first flooding. Thereafter, no *Silaum silaus* seeds and only 1.5 *Serratula tinctoria* seeds per planting site were found in the traps. No seedlings of either species emerged from 100 surrounding dung pats or from nearby drift lines which were examined to obtain further information about dispersal by cattle and by water.

### 3.3. Seedling survival

Foury-five percent of *Silaum silaus* seedlings that emerged around the planting sites of “restoration grassland” in May 1999 survived until September of the following year (Table 3). Within this period the survival of seedlings in “old grassland” was 23%. The majority of seedlings died in the first vegetation period up to September 1999. The differences in seedling survival between the two grassland types were not significant.

At the same time, survival of *Serratula tinctoria* was 54% in “restoration grassland” and 30% in “old grassland”. In both grassland types a comparably high proportion of seedlings survived the first vegetation period.

![Graph showing seedling density for *Silaum silaus* and *Serratula tinctoria*.](image)

**Fig. 3.** Spatial distribution of *Silaum silaus* and *Serratula tinctoria* seedlings around introduced parent plants; experiment 2: usual management; *n* = 4.

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**Table 3**

Survival of *Silaum silaus* and *Serratula tinctoria* seedlings after the first (09/1999) and the second (09/2000) vegetation period

<table>
<thead>
<tr>
<th>Survival rates</th>
<th>Deviance</th>
<th>d.f.</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>OG</td>
<td>RG</td>
<td>Change</td>
</tr>
<tr>
<td><em>Silaum silaus</em></td>
<td>09/1999</td>
<td>0.36</td>
<td>0.68</td>
</tr>
<tr>
<td></td>
<td>09/2000</td>
<td>0.23</td>
<td>0.45</td>
</tr>
<tr>
<td><em>Serratula tinctoria</em></td>
<td>09/1999</td>
<td>0.72</td>
<td>0.75</td>
</tr>
<tr>
<td></td>
<td>09/2000</td>
<td>0.30</td>
<td>0.54</td>
</tr>
</tbody>
</table>

NS, not significant.

* Differences between “old” (OG) and “restoration grassland” (RG) were tested in a generalized linear model (binomial error) using the F-test to analyse changes in deviance
(75 and 72%). Again no significant differences were found between “restoration grassland” and “old grassland”. Plants of both *Silaum silaus* and *Serratula tinctoria* were still very small after 1.5 years (≤3 leaves) and did not attain the reproductive stage.

4. Discussion

After 10 years of extensive management the species composition of “restoration grassland” was still very different from grassland never managed intensively (“old grassland”). Characteristic floodplain grassland species such as *Silaum silaus, Serratula tinctoria, Sanguisorba officinalis, Allium angulosum* and *Thalictrum flavum*, did not reappear in “restoration grassland” although large populations occurred in adjacent “old grassland”. Similar patterns were found for other wet grassland types (Bakker, 1989; Kapfer, 1994; McDo-nald et al., 1996) and for chalk grassland (Graham and Hutchings, 1988).

4.1. Conditions of establishment

Since hydrological conditions were standardized by selecting sites of the same altitude and groundwater level, soil conditions were the most important factors which could determine re-establishment. In particular, the depletion of fertilizer residues may require more than 10 years (Gough and Marrs, 1990; Willems and Nieuwstadt, 1996; Tallowin et al., 1998). Although overall P and K values were higher in “restoration grassland” than in “old grassland”, the differences were small and phosphorous content was not higher in the topsoil, which is most relevant for grassland species. Nitrogen content was even lower in “restoration grass-

land” than in “old grassland” probably because former arable cultivation had reduced the organic nitrogen pool. Gough and Marrs (1990) found that grassland recently converted from arable fields contained less organic matter resulting in lower amounts of inorganic N derived from mineralization. Altogether, it seems unlikely that the measured differences in soil chemistry were the reason for the failure in re-establishment of characteristic species. The bulk density was also similar indicating comparable aeration in “restoration” and “old grassland”.

However, it is not possible to measure all factors that may influence re-establishment, so studies on the survival of seedlings were additionally used as a bioassay of abiotic site conditions. Although none of the seedlings reached the reproductive stage within two seasons, the similar survival rates of *Silaum silaus* and *Serratula tinctoria* strongly suggests that there are no differences in establishment between “restoration grassland” and “old grassland”.

4.2. Dispersal limitation

In the dispersal experiments seeds of *Silaum silaus* and *Serratula tinctoria* were dispersed very short distances. Most seedlings were found within a radius of 1.5 m of parent plants and a very small proportion of seeds was dispersed beyond 3 m. The transect analysis confirmed the results of dispersal experiments. *Silaum silaus, Serratula tinctoria* and the less abundant characteristic species (*Sanguisorba officinalis, Allium angulosum, Thalictrum flavum*) were restricted to areas near seed sources in “old grassland”. The results strongly suggest that poor dispersal was the main limiting factor in re-establishment of these species in “restoration grassland”. They support grassland studies of van Groenendael (1989) and Kapfer (1994) who also came to the conclusion that the restoration of their study sites was limited by dispersal although dispersal was not directly analysed.

Several authors highlight the importance of management for dispersal in grasslands. Firstly, the mowing machinery may be an efficient dispersal vector (Strykstra et al., 1997). Secondly, many plant species can be dispersed by grazing livestock (Poschlod and Bonn, 1998). If seeds survive digestion the endozoochorous dispersal is very effective because gaps created by dung pats improve seedling establishment (Malo and Suarez, 1995; Humphreys et al., 1997). Distances of epizoochorous transport of seeds may be very large but most species are only dispersed in small numbers (Fischer et al., 1996). In this study, management did not increase dispersal distances. Seed shadows of *Silaum silaus* and *Serratula tinctoria* in “restoration grassland” managed by grazing and cutting were very similar to unmanaged planting sites outside the floodplain. Dispersal by mowing machinery was not possible because...
the grass was cut in early June whereas *Silaum silaus*, *Serratula tinctoria* and the other characteristic species start to reproduce in August. Since the grazing period is the late summer and parent plants of the dispersal experiment were eaten, cattle are a potential dispersal vector. However, no *Silaum silaus* and *Serratula tinctoria* seedlings were recorded in the surrounding dung pats. This result and the similarity of seed shadows around managed and unmanaged planting sites indicate that cattle are of minor importance in dispersing these species. However, a sporadic transport of seeds cannot be entirely excluded.

Several studies have found hydrochory to be important in dispersing floodplain plant species. Many species are recorded in litter material of drift lines created by flooding (Hughes and Cass, 1997; Andersson et al., 2000). Johansson et al. (1996) came to the conclusion that water dispersal affects the structure of riparian flora and can explain distribution patterns. However, information about dispersal distances of particular species is scarce. During periods of inundation of the Saale River floodplain the water usually moves very slowly and the movement is mainly caused by the wind. This could explain the similarity of seed shadows in the dispersal experiments in and outside the floodplain. The absence of *Silaum silaus* and *Serratula tinctoria* seedlings in nearby drift lines also indicates that flooding was ineffective in dispersing the species. Although hydrochorous long-distance transport cannot be entirely excluded, spatial distribution of seedlings around the parent plants suggests that wind was the main dispersal vector in the dispersal experiments.

4.3. Conclusions and implications for nature conservation

The results indicate that suitable abiotic site conditions cannot guarantee successful restoration of floodplain grassland because dispersal may be the limiting factor of re-establishment. To model restoration processes, the distance and number of seed sources in relation to the dispersability of key species must be explicitly considered. This study also supports results of Bakker (1989) and van Groenendael (1989), who found that seedling survival in grasslands is even low if site conditions are favourable. Therefore, a large initial input of seeds may be necessary to establish new populations.

In nature conservation practice these results can help to predict chances of re-establishment if the positions of source populations are known. Since financial support for restoration measures is only available for a limited number of farmers, this information is important for the selection of suitable sites. However, much more research on dispersal and seedling establishment is required to target suitable sites effectively.

There are three strategies to overcome the mentioned obstacles of re-colonization and therefore to accelerate restoration processes:

1. Artificial re-introduction. Manchester et al. (1998) were quite successful in recreating a wet grassland community on ex-arable land by sowing seeds. However, re-introduction is expensive, many rare species are not commercially available and the preference for local provenance (pure seeds, cuttings, plants) may considerably increase the costs.

2. Improvement of dispersal. Since cattle were not efficient in dispersing *Silaum silaus* and *Serratula tinctoria* it may be possible to aid dispersal by replacing grazing by a second cut. Therefore, further research on transport of seeds by mowing machinery is necessary.

3. The increase of establishment rates. The creation of gaps into grassland swards probably increases the establishment of seedlings. The effect of different methods (opening of swards by machines, trampling of cattle) on establishment rates should be studied.

Acknowledgements

For her help in preparing the soil samples and for the analysis of C, and N I thank A. Thondorf. N$_{\text{min}}$ was analysed by the Department of Soil Science (E. Rohländer) and extractable P and K by the Department of Analytical Chemistry (J. Steffen) of the Centre for Environmental Research (UFZ). Thanks are expressed to H. Auge, W. Durka, D. Prati, S. Klotz, D. Tucker, S. Merrit, B. Davis and an anonymous reviewer for helpful comments on the manuscript. The research was financed by the Deutsche Forschungsgemeinschaft (DFG).

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