Applied Vegetation Science 6: 131-140, 2003

Restoration of a species-rich flood meadow by topsoil removal and diaspore transfer with plant material

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Abstract. In previous studies, limited dispersal was revealed to be the main obstacle to restoration of species-rich flood-meadows along the northern Upper Rhine in Germany. To overcome dispersal limitation we transferred freshly mown plant material from species-rich sources to a restoration site on a former arable field. Before plant material application, topsoil was removed to accelerate nutrient impoverishment and create favourable conditions for seedling recruitment.

Topsoil removal led to a drastic reduction in organic matter and essential mineral nutrients to the level of target communities (P) or even below (N, K). At a removal depth of 30 cm content of the soil seed bank that comprised exclusively of annual arable weeds, ruderals and some common grassland species, declined by 60 - 80%, while at a removal depth of 50 cm the seed bank was almost completely eliminated. With few exceptions, all species recorded in source plant material were found established at the restoration site. However, the overall correlation between seed content in plant material and establishment success was not very high.

Vegetation development at the restoration site was characterized by a rapid decline in arable weeds and ruderals, while resident grassland species and species transferred with plant material increased rapidly from the third year onwards. After four years as many as 102 species were established that could be exclusively attributed to plant material transfer, among them many rare and highly endangered plants. Establishment of species from plant material was most successful in regularly flooded plots, due to the suppression of competitors as well as the creation of favourable moisture conditions for seedling emergence.

Diaspore transfer with plant material proved to be an extremely successful method in restoring species-rich grassland. However, high quality of plant material and suitable site conditions with low competition in early stages of succession seem to be essential prerequisites.

Keywords: Biodiversity; *Cnidion*; Dispersal limitation; Grassland; *Molinion*; Nature conservation; Path analysis; Seedling recruitment; Seed bank.

Nomenclature: Wisskirchen & Haeupler (1998).

Introduction

In Central Europe, flood meadows of the *Cnidion* alliance are strictly confined to large lowland river corridors with subcontinental climatic conditions such as the valleys of the rivers Rhine, Elbe and Danube (Burkart 2001). Due to flood control, drainage, intensified use and conversion into arable land such habitats have become extremely rare and a considerable part of the characteristic flora such as *Arabis nemorensis, Cnidium dubium, Iris spuria* and *Viola pumila* has been categorized as species of Central European conservation concern (Schnittler & Günther 1999). Remnant populations of these highly endangered species are still found along the northern Upper Rhine, where they exist in mesotrophic *Cnidion* and in oligotrophic alluvial *Molinion* communities (Böger 1991; Hölzel 1999). In this region, large-scale restoration efforts aimed at the recreation of species-rich flood meadows at sites of former arable fields have been pursued for more than 15 yr (Hölzel et al. 2002). A recent evaluation of these restoration measures revealed very poor success in re-establishing rare and endangered target species and communities, even at sites with successful lowering of soil nutrient status and productivity by regular mowing and haymaking without fertilizer application (Donath et al. 2003). These findings are in accordance with earlier studies on grassland restoration that identified the lack of viable seeds in the soil seed bank and limited dispersal of target species as the main constraints to restoration of species-rich grassland (Bakker 1989; Berendse et al. 1992; Hutchings & Booth 1996; Bakker et al. 1996; Pegtel et al. 1996; Muller et al. 1998; Bakker & Berendse 1999). All these studies revealed that low productivity is essential but that restoration success cannot be guaranteed in the absence of substantial seed resources. Analogous results were obtained in seed addition experiments that confirmed recruitment limitation as an important factor governing species-richness in grassland (Tilman 1997; Stampfli & Zeiter 1999; Turnbull et al. 2000; Pywell et al. 2002; Smith et al. 2002).

In previous years, diaspore transfer with plant material has been increasingly tested as a supplementary technique in restoration ecology to overcome dispersal limitation of target species. Such measures showed considerable, but not always compelling, success (McDonald 1993; Molder 1995; Biewer 1997; Tränkle 1997; Patzelt 1998; Pfadenhauer & Miller 2000; Kirmer & Mahn 2001). In fact, plant material (or hay) transfer is an old and traditional method widely used by farmers until the middle of the 20th century to create and improve grassland (Bonn & Poschlod 1998). The fact that this agricultural practice ceased in modern times is often regarded as one main reason for dispersal limitation of species in agricultural habitats (Bakker et al. 1996).

In comparison with direct sowing of seeds, the application of diaspores with plant material in habitat restoration has a number of advantages: (1) potentially, the entire species-pool of a plant community may be covered by material transfer, including rare species of which sowing material is often not available; (2) the genetic variability of locally adapted ecotypes and races is preserved and maintained (e.g. Molder 1995; Pegtel 1998); (3) on bare substrates with extreme micro-climatical conditions plant material may provide 'safe sites' for seedling recruitment (Patzelt 1998; Tränkle 1997); (4) compared to the relatively laborious and expensive collection, propagation and sowing of seeds (e.g. Stevenson et al. 1995), diaspore transfer with plant material is a cheap method that is applicable to large areas and different types of habitats. Despite these benefits, however, large-scale practical applications in restoration projects (e.g. Pfadenhauer & Miller 2000) are still scarce. Most previous work was conducted as small-scale studies that often comprised only of a few dozen m^2 (Molder 1995; Kirmer & Mahn 2001). For many habitat types and species groups – such as the rare subcontinental flood-meadows – experience regarding the effectiveness of plant material transfer is still completely lacking.

Factors that may hamper the success of plant material transfer experiments are: (1) low quality of plant material in terms of species composition and seed densities, (2) unfavourable target site conditions (soil nutrient status, moisture regime), (3) poor conditions for seedling recruitment due to dense canopy structure of established vegetation, (4) adverse weather conditions (drought, frost) during the germination period causing high seedling mortality. Generally, the relative importance and interaction of these potentially hampering factors are strongly context dependent so that it is difficult to define common rules and guidelines without large-scale field evidence (Bosshard 1999).

Recently, topsoil removal has been revealed as a very effective measure to increase the impoverishment of nutrient enriched sites, by combining bare substrate with poor competition (Aerts et al. 1995; Jansen & Roelofs 1996; van Diggelen et al. 1997; Patzelt et al. 2001; Tallowin & Smith 2001; Verhagen et al. 2001). Thus, we used this technique in combination with plant material transfer to create favourable site conditions for seedling recruitment. Additional positive effects we expected were: (1) increase of flooding frequency due to surface lowering, (2) depletion of the soil seed bank and the established vegetation, (3) re-activation of deeply buried viable seeds of target species.

Due to the high heterogeneity in seed content and species composition of plant material it is not feasible to perform well defined factorial experiments with true replicates in randomized order (e.g. Molder 1995; Bosshard 1999). The main object of our study, however, was not to test a mechanistic hypothesis of universal validity, but rather to evaluate the efficiency of material transfer as a method for restoration practice. Thus we chose an observational approach that allowed us to conduct our study on a large scale and under a realistic practical scenario.

To assess the influence of plant material transfer on succession we separately analysed the two major compartments of the species pool, i.e. plant material and soil seed bank, and observed the vegetation development with different treatment variants over four years. Furthermore, we investigated the effects of topsoil removal on soil nutrient status by comparing the original arable field with removal plots and source stands.

Material and Methods

Study site

The study site is a former arable field (1.3 ha) situated in the fossil dyke-protected compartment of the Holocene floodplain of the northern Upper Rhine ca. 30 km southwest of Frankfurt, Germany (49°51' N, 8°23' E, 85 m a.s.l.). The hydrological site conditions are characterized by strong fluctuations of the ground water table, which are in the region of 2 m per year (Böger 1991) depending on the water level of the nearby (ca. 300 m) main channel of the River Rhine. Due to extremely high clay content the soil shows some unfavourable physical features such as poor aeration in wet periods, low storage capacity of plant available water and hardening in summer. During the observation period major flooding events, that lasted for several weeks, occurred in March and May/June 1999 and in March/April 2001, whereas dry periods were observed every summer from early May onwards.

Restoration measures

For more than 20 yr the study site was intensively used as an arable field until it fell fallow for nature conservation purposes in 1994. In late August 1997, the nutrient-rich topsoil was removed from almost the entire field (ca. 1.3 ha) down to a depth of 30 or 50 cm (Fig. 1). After topsoil removal the area was subdivided into eight parallel strips, each 20 m × 50 m.

September was chosen as the date of transfer, because at this time the majority of target species had ripe seeds while most of the dominant grasses (e.g. *Alopecurus pratensis*) had already released their seeds (Hölzel unpubl.). Two different types of material were used in the experiment (Fig. 1b):

1. Alluvial *Molinion* meadows are exclusively found at regularly flooded extremely nutrient-poor sandy sites where the loam cover was removed in the past. They are floristically characterized by a strictly oligotrophic species composition with *Molinia caerulea* agg., *Carex panicea*, *Serratula tinctoria, Inula salicina* and *Succisa pratensis* dominating. Due to extreme site conditions they are species-poor with less than 30 species.100m^{-2}. Some target species such as *Gentiana pneumonanthe, Dactylorhiza incarnata* and *Iris sibirica* are restricted to this vegetation type.

2. In contrast, *Cnidion* meadows occupy more fertile loamy and clay-rich sites, which are also regularly flooded. They are characterized by a higher proportion of nutrient-demanding meadow species such as *Alopecurus pratensis, Elymus repens* and *Potentilla reptans*. However, they share many target species with the *Molinion* meadows such as *Arabis nemorensis, Pseudolysimachion longifolium, Serratula tinctoria* and *Inula salicina*. In general, they are more species-rich with 40 - 60 species.100m^{-2}. *Cnidion* material from a particular salt-influenced site that contained the rare *Iris spuria* and some other salt-tolerant species such as *Lotus tenuis* and *Tetragonolobus maritimus* was only brought to strip I.

Four strips in early September 1997 and two strips in 1998 were covered with freshly mown plant material from nearby remnants of species-rich flood-meadows, while two strips remained without treatment (indicated zero). Plant material was harvested with conventional hay making machinery and spread manually at the restoration site in a loose 5 to 10 cm thick layer.

The whole site was mown yearly in September with a flail mower to prevent the emergence of woody plants. Because of the low production biomass was not removed.

Vegetation sampling

Each of the eight 20 m × 50 m treatment strips was subdivided into ten 10 m × 10 m quadrats (80 quadrats in total, Fig. 1). From 1998 onwards, vascular plants were recorded annually for the entire 10 m × 10 m quadrat. Species cover and abundance values were estimated visually using a modified Braun-Blanquet scale with cover value 2 subdivided into 2m, 2a and 2b (van der Maarel 1979). Vegetation of the source stands was recorded in the same way every year with six quadrats in each of the *Molinion* and *Cnidion* meadows.

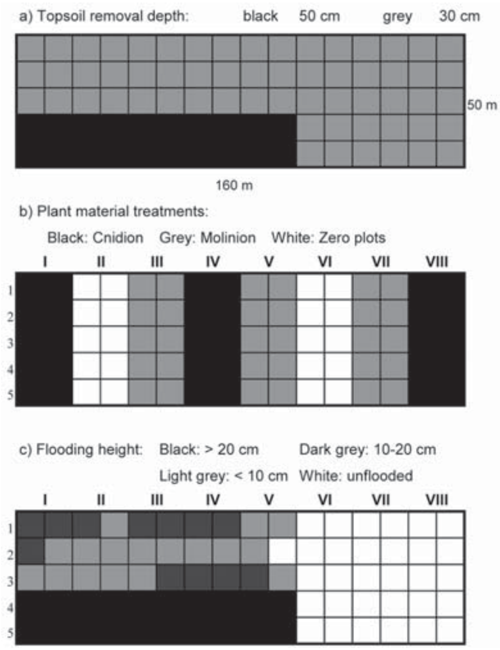

Fig. 1. Plan of study site and treatments.

Soil properties

To investigate the effects of topsoil removal, the following soil properties were measured: total nitrogen and organic carbon content, calcium-acetate-lactate (CAL) soluble phosphorus and potassium. Samples were taken from four plots with 30 cm, 50 cm and adjacent areas without topsoil removal, respectively. In each plot, five soil cores were taken at random locations at a depth of 0-10 cm using a 3 cm diameter corer, and subsequently pooled for analysis. The same method was applied to the 12 quadrats in the source stands to obtain a reference for the soil nutrient status in the target communities. Flooding frequency per plot was calculated using data from a neighbouring groundwater gauge, field observations and topography (Fig. 1c).

Seed bank sampling

To determine the influence of topsoil removal on the soil seed bank, and the potential role of buried seeds in succession, we studied soil seed bank composition in four plots with 30 cm, two plots with 50 cm and two plots without topsoil removal. In each plot, twenty 10 cm deep soil cores were taken in September 1997 at random locations with a 3 cm diameter corer. The seed bank samples represent 141 cm^2 of the soil surface and 1410 cm^3 of the soil volume at each plot.

Plant material sampling

To analyse the quantity and quality of transferred diaspores, at each of four treatment strips two samples of plant material were taken from the soil surface in February 1998 and 1999, five months after material application. Each sample comprised six quadrats of 31.6 cm by 31.6 cm that were taken with an iron frame at random locations and pooled together. Superficial plant material and 2 cm of the topsoil that was expected to contain discharged seeds were sampled and analysed separately. During this sampling in February, we did not find any seedlings under the plant material layer, which was in accordance with additional germination experiments (Hölzel unpubl.).

Analysis of seed contents

Seed bank composition in the soil and the plant material was analysed using the seedling emergence method (Roberts 1981). Soil samples were placed directly in a 2 - 3 cm thick layer in 18 cm × 28 cm styrofoam basins and exposed to free air conditions to enhance natural stratification. Plant material was mixed with sterile soil and exposed in the same way. The basins were protected against diaspore input and heating by covering them with flat, white gauze lids. In summer the basins were watered regularly. Control basins filled with sterile soil were used as spacers. Germinated seedlings were identified and removed every few weeks. Unidentifiable specimens were transferred to pots and grown until they could be identified. When germination declined the samples were dried in a greenhouse, crumbled, mixed, watered and exposed again to free air. The analysis of diaspore contents in soil and plant material continued for 36 months.

Data analysis

Plant species occurring at the restoration site were grouped in the following categories:

1. Annual arable weeds: Present in soil seed bank and/or established vegetation over the entire restoration site (including control plots) and/or its direct periphery in the first season with sharp decline in the second season; absent from source stands.

2. Perennial or biennial ruderals: As (1) but still frequent in second year of observation; absent from source stands with few exceptions (e.g. *Cirsium arvense*).

3. Resident grassland species: As (2) but typical of established grassland in the region. Although most of these species, such as *Festuca arundinacea, Poa trivialis, Achillea millefolium* and *Plantago lanceolata*, also occurred in source stands and thus may be part of the plant material fraction, they were exclusively included in this group.

4. Plant material species: Present in source stands, exclusively found at plant material treatments and completely absent from control plots in the first two seasons, absent from soil seed bank and the direct periphery of the restoration site.

Linear regression was used to assess the relationship between seed contents of species in plant material and their establishment success as well as to test the causal influence of flooding and groups of competitors on establishment success of plant material species. To separate the direct and indirect causal covariation of flooding on establishment success we used the method of path analysis (Legendre & Legendre 1998, pp. 546-551), which was performed on standardized variable values.

Means of soil nutrient variables were compared using the parametric Tukey Honest-Significance (HSD) test for unequal sample sizes. Regressions and ANOVA were performed on log-transformed data matrices using STATISTICA 6.0.

Results

Effects of topsoil removal on soil nutrient status

Topsoil removal had large effects on soil nutrient status at the restoration site (Fig. 2). In the case of available P there was a sharp decline to the level of species-rich old stands of *Cnidion* meadows or even *Molinion* meadows (50 cm removal depth). Available K, total N and organic matter ranged even below the values found in the source communities. All effects were most pronounced at a soil removal depth of 50 cm.

Effects of topsoil removal on soil seed bank

The size of the soil seed bank, which reached up to 12000 seed.m^{-2} in the young fallow arable field, declined dramatically after topsoil removal (Fig. 3). At a removal depth of 30 cm only 20 - 40% of the former values were found, while at a removal depth of 50 cm the soil seed bank was almost completely eliminated. Seed bank composition was dominated by typical annual arable weeds such as *Chenopodium polyspermum, C. album, Erucastrum gallicum, Sonchus asper* and

Stellaria media. However, we also found a considerable number of seeds of some common perennial meadow species such as *Poa trivialis, Achillea millefolium, Galium album* and *Medicago lupulina*. These may play an essential role even in advanced successional stages of meadow communities. No seeds of rare or endangered target species of flood-meadows were recorded.

Seed contents in plant material

A total of 19394 individuals of 66 species that could exclusively be accounted to transfer (species group 4) were found in the analysis of sampled plant material (App. 1). In general the results displayed a considerable variation and patchiness in species distribution and seed densities between and even within material of the same origin. Total densities of plant material species usually ranged between 551 and 2125 seed.m^{-2}. In one case we found an exceptionally high density of 24019 individual.m^{-2} to which a single species, *Pseudolysimachion longifolium*, contributed > 80%. Species numbers in *Cnidion* samples ranged from 22 - 28 species.m^{-2} while they were lower in samples from *Molinion* stands with only 15 - 17 species.m^{-2}. Maximum densities of more than 100 individual.m^{-2} were reached by only nine species, among them some rare and endangered target species such as *Pseudolysimachion longifolium, Arabis nemorensis* and *Inula salicina*. In contrast, the majority (38 species) had maximum densities of only ten or less individuals per m^2. Compared to their dominant role in the source stands, grasses and sedges (except *Agrostis stolonifera*) were very under-represented in plant material. This phenomenon was also reflected in vegetation development.

Vegetation development

In the first year of observation, the vegetation at the restoration site was still dominated by ruderals and annual arable weeds that emerged from the soil seed bank and shoots remaining after topsoil removal (Fig. 4). From the second year onwards, annual arable weeds disappeared almost completely from the established vegetation, while the decline in ruderal species was more continuous over the years. In contrast, an increase in total cover of plant material species and resident grassland species was observed in the third year. While total number and frequency of resident grassland species remained almost constant, there was a sharp increase in species originating from plant material. After 4 yr, 102 species that could be

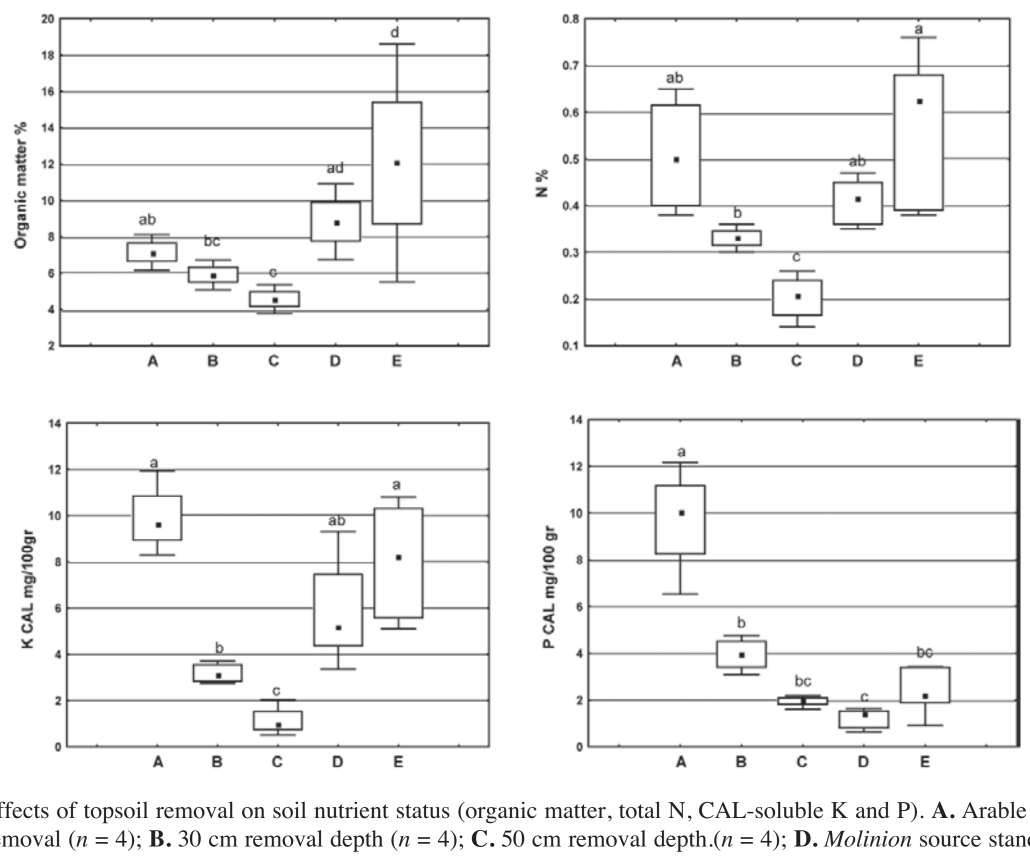

Fig. 2. Effects of topsoil removal on soil nutrient status (organic matter, total N, CAL-soluble K and P). **A.** Arable field without topsoil removal (n = 4); **B.** 30 cm removal depth (n = 4); **C.** 50 cm removal depth.(n = 4); **D.** *Molinion* source stands (n = 6); **E.** *Cnidion* source stands (n = 6). Significant differences according to the Tukey Test are indicated by different letters.

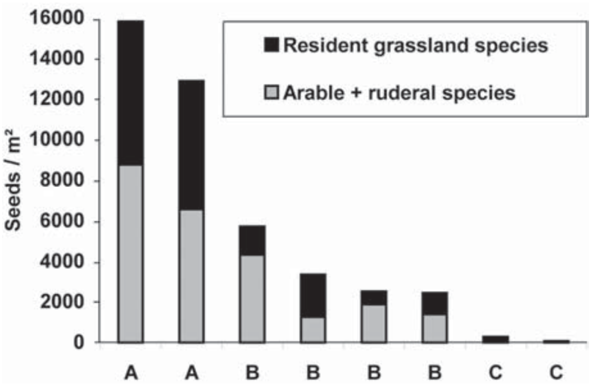

Fig. 3. Effect of topsoil removal on the size of the soil seed bank at the restoration site. Samples originating from: A = Arable field without topsoil removal; B = 30 cm removal depth; C = 50 cm removal depth.

exclusively accounted to plant material transfer were found at the restoration site (Fig. 4; App. 2). Among these were 31 species mentioned in the national German and regional Hessian Red Data Book (Korneck et al. 1996). Species derived from plant material comprised 64% of all species found in established vegetation in 2001 and 49% of all species observed during the entire observation period. Transfer rates (i.e. the number of species that established from plant material at the restoration site as a percentage of the number of species that occurred in the source stands) for single strips ranged from 64% to 72% for the wet (flooded) strips and from 53% to 56% for the dry (not flooded) strips (Table 1). In total 82% of the entire species pool at the source sites was transferred after four years.

Simple linear regression between species recorded in plant material (all analysed samples pooled) as the independent variable and established vegetation in the fourth year of observation (only strips with material sampling) as the dependent variable resulted in a considerable proportion of explained variance ($r^2 = 0.32$, $P < 0.001$). Of the species recorded in plant material, only *Carex praecox, C. tomentosa* and *C. otrubae* did not establish during the study. With few exceptions, such as the legumes *Genista tinctoria*, *Ononis spinosa* and *Lotus tenuis,* species not recorded in the plant material

Table 1. Transfer rates and efficiency of plant material (pl. mat.) analysis in the different treatments. In strips V and VII seed contents in plant material were not measured (n.m.)

Strip	I	III	IV	V	VII	VIII
No. of species at source sites	97	74	84	81	75	77
No. of established species	70	48	54	54	42	41
Transfer rate in %	72	65	64	67	56	53
No. of spec. in pl. mat.	38	21	24	n.m.	n.m.	28
% transferred spec. in pl. mat.	54	44	44	n.m.	n.m.	62

analysis (App. 1) were also scarce and infrequent in established vegetation (App. 2). Generally, the invasion of species from plant material treatments to neighbouring control treatments occurred much faster in the case of the wet, regularly flooded plots (Fig. 5, App. 2).

Simple linear regressions of all plots with material application ($n = 60$) revealed a strong negative correlation between the cover of resident grassland species and the cover of species that emerged from plant material (Fig. 6). On the other hand, there was a positive correlation between the cover of plant material species and flooding height, and a negative correlation between flooding height and the cover of resident grassland species. Although decomposition of direct and indirect causal influence of flooding on establishment success by path analysis (Fig. 6) suggested a relatively high proportion of indirect causal covariation via competitors, there nevertheless remained a considerable proportion of direct covariation.

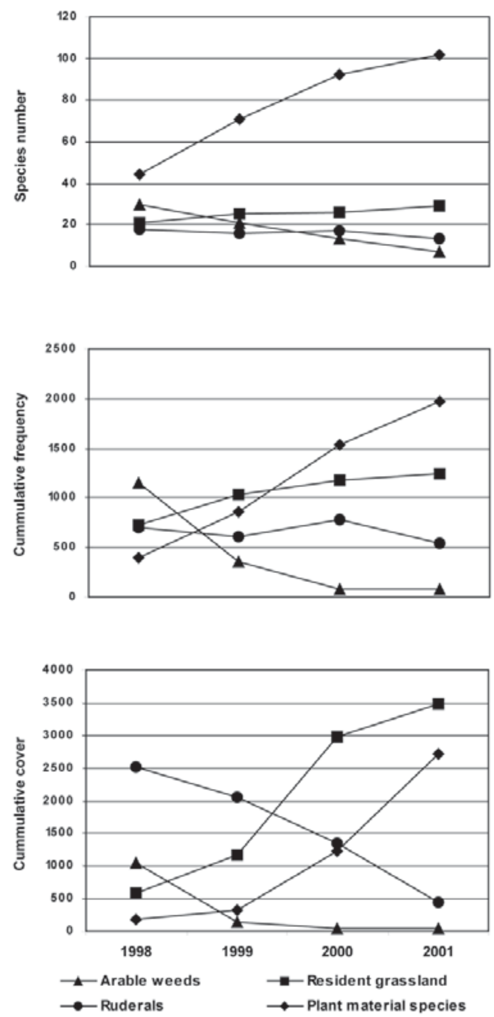

Fig. 4. Development in species number, cumulative frequency and cover of different species groups at the entire restoration site between 1998 and 2001. All plots (n = 80) pooled.

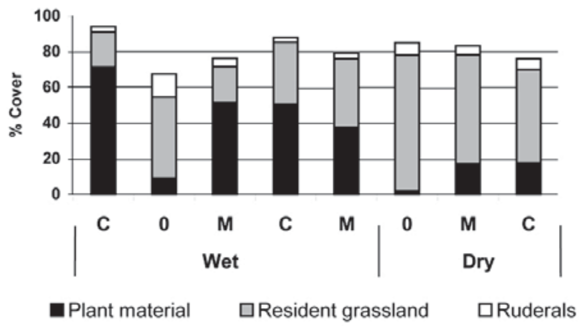

Fig. 5. Cumulative cover of different species groups along the treatment strips four years after plant material application. C = *Cnidion* material; M = *Molinion* material; 0 = Control treatments. Wet = regularly flooded strips; Dry = never flooded strips.

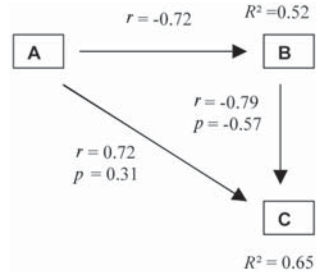

Fig. 6. Decomposition of direct and indirect causal influence of flooding on establishment success of plant material species: A = flooding height; B = cover of resident grassland species in 2001; C = cover of plant material species in 2001; r = covariation in simple linear regression, p = parameter estimate in multiple regression, R^2 = explained variance; all values significant ($p < 0.01$).

Discussion

Effects of plant material transfer

In the present study diaspore transfer with plant material proved to be a very effective method to overcome dispersal limitation of rare and endangered target species in habitat restoration. Our results are in accordance with seed addition experiments (e.g. Burke & Grime 1996; Tilman 1997; Pywell et al. 2002) that found species diversity in plant communities to be strongly governed by recruitment limitation, most commonly in early successional stages (Turnbull et al. 2000). The transfer rate was particularly high compared to other plant material transfer experiments (Tränkle 1997; Patzelt 1998; Pfadenhauer & Miller 2000). Total seed densities per m^2 in plant material ranged considerably below those recommended in practice for the recreation of species-rich grassland (Smith et al. 1997; Bosshard 1999; Pywell et al. 2002). Surprisingly, even species with maximum densities of less than 10 seed.m^{-2} in plant material, which is two orders of magnitude lower than the rates normally used in seed addition experiments (Turnbull et al. 2000), established successfully. Seed content in plant material alone proved to be a weak predictor for establishment success and may be strongly outweighed by colonization ability in certain species (e.g. Patzelt 1998). Low densities of grasses and sedges in plant material were also reported from other transfer experiments (Patzelt 1998; Pfadenhauer & Miller 2000), which is obviously mostly due to late mowing (Biewer 1997). Principally, this bias towards herbaceous species should not be seen as a disadvantage, since the establishment of target species is usually facilitated by a low abundance of strongly competitive grasses (e.g. Lepš 1999) and a delayed development of a closed sward (e.g. Bosshard 1999).

In accordance with other transfer experiments (e.g. Patzelt 1998; Pfadenhauer & Miller 2000), species with preferably vegetative means of spread and poor regeneration by seeds, such as the genus *Carex* (Grime et al. 1998; Schütz 2000), were predominant among those failing to establish from plant material.

Effects of topsoil removal

The success that was achieved must be seen in conjunction with topsoil removal that created the most favourable conditions for seedling recruitment. However, even in the present study, establishment success of species from plant material was revealed to be strongly correlated with the degree of competition from established vegetation (Fig. 6). In many experimental studies (e.g. Tilman 1993; Rusch & Fernandez-Palacios 1995; Křenová, Z. & Lepš 1996; Kotorová & Lepš 1996, 1999) microsite limitation and competition from established plants proved to be the main constraints governing germination, growth and survival of seedlings. Due to the partial depletion of the soil seed bank and established vegetation by topsoil removal the temporal and spatial dimension of the 'regeneration niche' (Grubb 1977) as a 'window in time' (Gross & Werner 1982) was considerably enlarged.

Besides the creation of open substrate with low competition, topsoil removal was absolutely essential for the reduction of available P to the level of the target communities. This was of particular relevance for the successful establishment of 'stress-tolerators´ (Grime 2001) that strictly depend on nutrient-poor site conditions, such as *Gentiana pneumonanthe* and *Succisa pratensis*, which are typical of *Molinion* meadows. Our findings are in accordance with many other studies that identified P as the major nutrient that may potentially hamper the re-establishment of low productive species-rich grassland communities (Egloff

1983; Gough & Marrs 1990; Oomes et al. 1996; Snow et al. 1997; Tallowin et al. 1998; Olde Venterink et al. 2001).

The rapid decline of ruderals – in comparison with other old-field successions (e.g. Schmidt 1993) – was obviously also an effect of the massive reduction in soil nutrient status, since the ruderal strategy is supposed to play an important role only under relatively fertile site conditions (Grime 2001). However, the negative impact of ruderals on establishment success was less significant than expected, as was also found by other authors (Bosshard 1999; Pfadenhauer & Miller 2000). In contrast, resident mesophyllous grassland species were revealed to be the most prominent group that may seriously hamper recruitment from plant material, although their vitality was considerably reduced by lowering the soil nutrient content.

Increased flooding frequency due to surface lowering had an unexpectedly large influence on the establishment success of plant material species, not only by the weakening of competitors. Under the given climatic (dry and warm) and edaphic (heavy, rapidly hardening clay soils) situation, seedling recruitment seems to be strongly facilitated by floods in late spring and early summer that provide favourable moisture conditions. In summer 1999, we found mass germination and rapid seedling development on muddy surfaces created by slowly retreating flooding water. Our findings are supported by many other studies that identified drought as a main source of germination failure (Baskin & Baskin 2001) and high seedling mortality (Cavers & Harper 1967; Silvertown & Dickie 1980; Ryser 1993). One might argue that additional species preferring wet site conditions were favoured by flooding and thus caused a bias towards higher establishment rates. However, we observed a general facilitation in establishment of plant material species by flooding, even in mesophyllous grassland species such as *Leucanthemum vulgare* and *Centaurea jacea*. The faster invasion of plant material species to regularly flooded zero plots underpins the significant role of flooding events for dispersal over moderate distances (Hölzel & Otte 2001).

Acknowledgements. We are grateful to a number of people who supported us during field work and in the lab; namely Tobias Donath, Lorenz Geißler, Petra Göbel, Ines Klingshirn, Josef Scholz vom Hofe, Jan Thiele and Kerstin Wahl. Tobias Donath, Lutz Eckstein and Rod Snowdon provided helpful comments to a former manuscript and polished our English. J.P. Bakker, as Coordinating Editor, and two anonymous referees greatly improved the quality of this paper with their comments. Our investigations were partly supported by grants from the Regional Hessian State Agency for Nature Conservation (Obere Naturschutzbehörde, RP Darmstadt) and the Federal German Agency for Nature Conservation (BfN).

References

Aerts, R., Huizoons, A., van Oostrum, J.H.A., Van de Vijver, C.A.D.M. & Willems, J.H. 1995. The potential for heathland restoration on formerly arable land at a site in Drenthe, The Netherlands. *J. Appl. Ecol*. 32: 827-835.

Bakker, J.P. 1989. *Nature management by grazing and cutting*. Kluwer, Dordrecht, NL.

Bakker, J.P. & Berendse, F. 1999. Constraints in the restoration of ecological diversity in grassland and heathland. *Trends Ecol. Evol*. 14: 63-68.

Bakker, J.P., Poschlod, P., Strykstra, R.J., Bekker, R.M. & Thompson, K. 1996. Seed banks and seed dispersal: important topics in restoration ecology. *Acta Bot. Neerl*. 45: 461-490.

Baskin, C.C. & Baskin J. M. 2001. *Seeds. Ecology, biogeography, and evolution of dormancy and germination*. Academic Press, San Diego, CA, US.

Berendse, F., Oomes, H.J., Altena, H.J. & Elberse, W.Th. 1992. Experiments on the restoration of species-rich meadows in The Netherlands. *Biol. Conserv*. 62: 59-65.

Biewer, H 1997. *Regeneration artenreicher Feuchtwiesen im Federseeried*. Projekt Angewandte Ökologie 24, pp. 3-323, Landesanstalt für Umweltschutz Baden-Württemberg, Karlsruhe, DE.

Böger, C. 1991. Grünlandvegetation im Hessischen Ried. *Bot. Natursch. Hessen* Beih. 3: 1-285.

Bonn, S. & Poschlod, P. 1998. *Ausbreitungsbiologie der Pflanzen Mitteleuropas*. Quelle & Meyer, Wiesbaden, DE.

Bosshard, A. 1999. Renaturierung artenreicher Wiesen auf nährstoffreichen Böden. *Diss. Bot*. 303: 1-194.

Burkart, M. 2001. River corridor plants (Stromtalpflanzen) in Central European lowland: a review of a poorly understood plant distribution pattern. *Global Ecol. Biogeogr*. 10: 449-468.

Burke, M.J.W. & Grime, J.P. 1996. An experimental study of plant community invasibility. *Ecology* 77: 776-790.

Cavers, B.P. & Harper, J.L. 1967. Studies in the dynamics of plant populations. I. The fate of seeds and transplants introduced to various habitats. *J. Ecol*. 55: 59-71.

Donath, T., Hölzel, N. & Otte, A. 2003. The impact of site conditions and dispersal on restoration success in alluvial meadows. *Appl. Veg. Sci*. 6: xxx-yyy

Egloff, Th. 1983. Phosphorus as a prime limiting nutrient in litter meadows (*Molinion*). Fertilization experiment in the lower valley of the Reuss. *Ber. Geobot. Instit. ETH / Stift. Rübel* 50: 119-148.

Gough, M.W. & Marrs, R.H. 1990. A comparison of soil fertility between semi-natural and agricultural plant communities; implications for the creation of floristically-rich grassland on abandoned agricultural land. *Biol. Conserv*. 51: 83-96.

Grime, J.P. 2001. *Plant strategies, vegetation processes and ecosystem properties*. 2nd. ed. Wiley, Chichester, UK.

Grime, J.P., Hodgson, J. G. & Hunt, R. 1988. *Comparative plant ecology. A functional approach to common British species*. Unwin Hyman, London, UK.

Gross, K.L. & Werner, P.A. 1982. Colonizing ability of 'biennial' plant species in relation to ground cover: implication for their distributions in a successional sere. *Ecology* 63: 921-931.

Grubb, P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* 52: 107-145.

Hölzel, N. 1999. Flora und Vegetation der Auenwiesen im NSG 'Lampertheimer Altrhein' – eine aktuelle Zustandsanalyse mit Hinweisen zur zukünftigen Pflege und Entwicklung. *Jahrb. Natursch. Hessen* 4: 24-42.

Hölzel, N. & Otte, A. 2001. The impact of flooding regime on the soil seed bank of flood-meadows. *J. Veg. Sci.* 12: 209-218.

Hölzel, N., Donath, T., Bissels, S. & Otte, A. 2002. Auengrünlandrenaturierung am hessischen Oberrhein – Defizite und Erfolge nach 15 Jahren Laufzeit. *Schriftenr. Vegetationsk.* 36: 125-131.

Hutchings, M.J. & Booth, K.D. 1996. Studies on the feasibility of re-creating chalk grassland vegetation on ex-arable land. I. The potential roles of the seed bank and the seed rain. *J. Appl. Ecol.* 33: 1171-1181.

Jansen, A.J.M. & Roelofs, J.G.M. 1996. The restoration of Cirsio-Molinietum wet meadows by sod cutting. *Ecol. Eng.* 7: 279-298.

Kirmer, A. & Mahn, E.G. 2001. Spontaneous and initiated succession on un-vegetated slopes in the abandoned lignite mining area of Goitsche, Germany. *Appl. Veg. Sci.* 4: 19-27.

Korneck, D., Schnittler, M. & Vollmer, J. 1996. Rote Liste der Farn- und Blütenpflanzen (*Pteridophyta* et *Spermatophyta*) Deutschlands. *Schriftenr. Vegetationsk.* 28: 21-187.

Kotorová, I. & Lepš, J. 1999. Comparative ecology of seedling recruitment in an oligotrophic wet meadow. *J. Veg. Sci.* 10: 175-186.

Křenová, Z. & Lepš, J. 1996. Regeneration of a *Gentiana pneumonanthe* population in an ologotrophic wet meadow. *J. Veg. Sci.* 7: 107-112.

Legendre, P. & Legendre, L. 1998. *Numerical ecology*. 2nd. ed. Elsevier, Amsterdam, NL.

Lepš, J. 1999. Nutrient status, disturbance and competition: an experimental test of relationships in a wet meadow canopy. *J. Veg. Sci.* 10: 219-230.

McDonald, A.W. 1993. The role of seed-bank and sown seeds in the restoration of an English flood-meadow. *J. Veg Sci.* 4: 395-400.

Muller, S., Dutoit, T, Allard, D. & Grevilliot, F. 1998. Restoration and rehabilitation of species-rich grassland ecosystems in France: a review. *Restor. Ecol.* 6: 94-101.

Molder, F. 1995. Vergleichende Untersuchungen mit Verfahren der oberbodenlosen Begrünung unter besonderer Berücksichtigung areal- und standortbezogener Ökotypen. *Boden Landsch.* 5: 1-235.

Olde Venterink, M., Wassen, M.J., Belgers, J.D.M. & Verhoeven, J.T.A. 2001. Control of environmental variables on species density in fens and meadows: importance of direct effects and effects through community biomass. *J. Ecol.* 89: 1033-1040.

Oomes, M.J.M., Olff, H. & Altena, H.J. 1996. Effects of vegetation management and raising the water table on nutrient dynamics and vegetation change in a wet grassland. *J. Appl. Ecol.* 33: 576-588.

Patzelt, A. 1998. Vegetationsökologische und populationsbiologische Grundlagen für die Etablierung von Magerwiesen in Niedermooren. *Diss. Bot.* 297: 1-154.

Patzelt, A., Wild, U. & Pfadenhauer, J. 2001. Restoration of wet fen meadows by topsoil removal: vegetation development and germination biology of fen species. *Restor. Ecol.* 9: 127-136.

Pegtel, D.M. 1998. Rare vascular plants at risk: recovery by seeding? *Appl. Veg. Sci.* 1: 67-74.

Pegtel, D.M., Bakker, J.P., Verweij, G.L. & Fresco, L.F.M. 1996. N, K, and P deficiency in chronosequential cut summer dry grasslands on gley podzol after the cessation of fertilizer application. *Plant and Soil* 178: 121-131.

Pfadenhauer, J. & Miller, U. 2000. Verfahren zur Ansiedlung von Kalkmagerrasen auf Ackerflächen. *Angew. Landschaftsökol* 32: 37-87.

Pywell, R.F., Bullock, J.M., Hopkins, A., Walker, K.J., Sparks, T.H., Burke, M.J.W. & Peel, S. 2002. Restoration of species-rich grassland on arable land: assessing the limiting processes using a multi-site experiment. *J. Appl. Ecol.* 39: 294-309.

Roberts, H.A. 1981. Seed banks in soil. *Adv. Appl. Biol.* 6: 1-55.

Rusch, G. & Fernandez-Palacios, J.M. 1995. The influence of spatial heterogeneity on regeneration by seed in a limestone grassland. *J. Veg. Sci.* 6: 417-426.

Ryser, P. 1993. Influences of neighbouring plants on seedling establishment in limestone grassland. *J. Veg. Sci.* 4: 195-200.

Schmidt, W. 1993. Sukzession und Sukzessionslenkung auf Brachäckern – Neue Ergebnisse aus einem Dauerversuch. *Scripta Geobot.* 20: 65-104.

Schnittler, M. & Günther, K.-F. 1999. Central European vascular plants requiring priority conservation measures – an analysis from national Red Lists and distribution maps. *Biodiv. Conserv.* 8: 891-925.

Schütz, W. 2000. Ecology of seed dormancy and germination in sedges (*Carex*). *Perspect. Plant Ecol. Evol. Syst.* 3: 67-89.

Silvertown, J.W. & Dickie, J.B. 1980. Seedling survivorship in natural populations of nine chalk grassland plants. *New Phytol.* 88: 555-558.

Smith, H., McCallum, K. & MacDonald, D.W. 1997. Experimental comparison of the nature conservation value, productivity and ease of management of a conventional and a more species-rich grass ley. *J. Appl. Ecol.* 34: 53-64.

Smith, R.S., Shiel, R.S., Millward, D. Corkhill, P. & Sanderson, R.A. 2002. Soil seed banks and the effect of meadow management on vegetation change in a 10-year meadow field trial. *J. Appl. Ecol.* 39: 279-293.

Snow, C.S.R., Marrs, R.H. & Merrick, L. 1997. Trends in soil chemistry and floristics associated with the establishment of a low-input meadow system on an arable clay soil in Essex. *Biol. Conserv.* 79: 35-41.

Stampfli, A. & Zeiter, M. 1999. Plant species decline due to abandonment of meadows cannot be easily reversed by mowing. A case study from the Southern Alps. *J. Veg. Sci.* 10: 151-164.

Stevenson, M., Bullock, J.M. & Ward, L.K. 1995. Re-creating semi-natural communities: effect of sowing rate on establishment of calcareous grassland. *Restor. Ecol.* 3: 279-289.

Tallowin, J.R.B. & Smith, R.E.N. 2001. Restoration of a *Cirsio-Molinietum* fen meadow on an agriculturally improved pasture. *Restor. Ecol.* 9: 167-178.

Tallowin, J.R.B., Kirkham, F.W., Smith, R.E.N. & Mountford, J.O. 1998. Residual effects of phosphorus fertilization on the restoration of floristic diversity to wet hay meadows. In: Joyce, C.B. & Wade, P.M. (eds.) *European lowland wet grasslands: Biodiversity, management and restoration*, pp. 249-263. Wiley, Chichester, UK.

Tilman, D. 1993. Species richness of experimental productivity gradients: how important is colonisation limitation? *Ecology* 74: 2179-2191.

Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78: 81-92.

Tränkle, U. 1997. Vergleichende Untersuchungen zur Sukzession von Steinbrüchen in Südwestdeutschland und neue Ansätze für eine standorts- und naturgerechte Renaturierung. In: Poschlod, P., Tränkle, U., Böhmer, J. & Rahmann, H. (eds.) *Steinbrüche und Naturschutz. Sukzession und Renaturierung*, pp. 1-327. Ecomed, Landsberg, DE.

Turnbull, L.A., Crawley, M.J. & Rees, M. 2000. Are plant populations seed limited? A review of seed sowing experiments. *Oikos* 88: 225-238.

van der Maarel, E. 1979. Transformation of cover-abundance values in phytosociology and its effects on community similarity. *Vegetatio* 39: 97-114

van Diggelen, R., Bakker, J.P. & Klooker, J. 1997. Top soil removal: new hope for threatened plant species? In: Cooper, A. & Power, J. (eds.) *Species dispersal and land use processes,* pp. 257-263. Proceedings of the 6th annual conference International Association for Landscape Ecology (IALE), 9-11 September1997, Aberdeen, UK.

Verhagen, R., Klooker, J., Bakker, J.P. & van Diggelen, R. 2001. Restoration success of low-production plant communities on former agricultural soils after topsoil removal. *Appl. Veg. Sci.* 4: 75-82.

Wisskirchen, R. & Haeupler, H. 1998. *Standardliste der Farn- und Blütenpflanzen Deutschlands*. Eugen Ulmer, Stuttgart, DE.

Received 8 July 2002;
Revision received 14 January 2003;
Accepted 16 January 2003.
Coordinating Editor: J.P. Bakker.

For App. 1, 2, see JVS/AVS Electronic Archives; www.opuluspress.se/pub/archives/index.htm