

Impact of seed- and microsite-limitation on species diversity in fen grasslands

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General introduction

Temperate fen grasslands belong to the most variable ecosystems in Central Europe, characterized by a high dynamic of natural processes (Succow & Joosten 2001, Dierssen & Dierssen 2001). The historical development of fen grasslands is closely connected to human activities in the landscape. Different types of fen grasslands (e.g. hay meadows: Molinion-community; wet meadows and pastures: Calthion-community; mesotrophic fen grasslands: Caricion nigrae and Caricion davallinae) developed out of primeval alder carrs by clearing and subsequent mowing or grazing or by drainage of natural fens and bogs followed by agricultural use (Dierssen & Dierssen 2001). They remained as open (i.e. non-woodland) habitats due to continuous human impact and thus are sensitive to changes of human activities in the landscape (e.g. Pott 1995, Ellenberg 1996). Regarding species diversity of vascular plants, moderately grazed or mown fens belong to the most species rich plant communities in central Europe, but through several degradation pathways, they can also turn to extremely species poor communities within a short time (e.g. Rosenthal 1992). In Northern Germany, fen grassland communities were described and classified in detail in recent time (Dierssen et al. 1988, Voss 2001, Schrautzer 2004). Especially successional processes after abandonment were the focus of extensive research (e.g. Müller & Rosenthal 1998, Schrautzer & Jensen 1999).

Losses in species diversity in fen grasslands were observed during the last decades all over Europe (Wheeler 1988, Schrautzer & Wiebe 1993, Joyce & Wade 1998, Bakker & Berendse 1999). The main reason for this development is an alteration of agricultural use: Both intensification and abandonment of low productive sites have contributed to the sharp decline of fen grassland area and diversity (e.g. Berendse et al. 1992, Grootjans et al. 1996, Mountford et al. 2000). On fen grasslands, improved land use practices can only be carried out after drainage, which leads to a mineralisation of the peat and eventually to eutrophication (Schrautzer & Trepel 1997). Today, species rich fen grasslands are considered as one of the most endangered ecosystems in Europe.

Species rich fen grasslands are a part of the European cultural landscape and a product of a long history of traditional land use. They are objects of both natural and cultural heritage and deserve preservation and restoration as important functional and aesthetically valuable elements of the landscape (Succow & Joosten 2001). For some species, which are nowadays listed as rare or endangered (e.g. *Pedicularis palustris* L.), moderately used fen grasslands are the only appropriate secondary habitat while primary habitats (e.g. fens at the margins of intact raised bogs) disappeared in most parts of Central Europe during the transformation of the landscape by humans (Rosenthal & Fink 1996). The survival of such species is dependent on the continuous management of still existing fen grasslands and the creation of new appropriate habitats by the reintroduction of traditional forms of land use and the restoration of site conditions.

SEED- AND MICROSITE-LIMITATION

To explain the mechanisms affecting species losses and to develop methods restoring species diversity in fen grasslands we face first the necessity to study processes, determining and limiting the occurrence of species at a site (see also Oostermeijer 2003).

The basic concept of species ecology describes each habitat as a set of niches, specific for each species (Krebs 1972, Grubb 1977, Grime 1979). The description of a niche includes both abiotic factors and biotic interactions (e.g. Tilman 1988).

According to the species pool concept (Zobel 1992, 1997, Zobel et al. 1998), a specific set of species, which are capable to colonise specific habitat types, occurs in a region (regional species pool). Which part of this regionally available species pool is realized at a given site (local species pool) depends on different both dispersal-maintained and dispersal-independent processes (e.g. Vandvik & Goldberg 2005).

Seed- respectively dispersal-limitation of a population is assumed if a plant species failed to reach a sufficient site with an efficient amount of diaspores to found a stabile population (Münzbergová & Herben 2005). This type of limitation is directly related to the frequency / abundance of the species in the landscape, to its seed production, persistence ability in the soil seed bank, dispersal mode and the degree of habitat fragmentation (Ozinga et al. 2005). As dispersal processes are difficult to quantify, this kind of limitation can be detected indirectly by seed addition (Eriksson & Ehrlen 1992, Turnbull et al. 2000) or by comparing regional species pool and species diversity at a local site with respect to the degree of spatial isolation to potential source populations (Ozinga et al. 2005a).

If the occurrence of species is limited by the availability of opportunities (gaps) for establishment and growth and not by the presence of viable diaspores, we call this

phenomenon microsite-limitation (Eriksson & Ehrlén 1992, Münzbergová & Herben 2005). A special case occurs, if the niche of the mature plant differs significantly from the niche of the seedling and juvenile stage (regeneration niche). In this case, adult individuals might still persist at the site, but germination and establishment requirements might not be met and thus the population growth rate is less than one if some mortality of adult individuals occurs. In the long run, this situation leads to the extinction of the species at the site (Oostermeijer et al. 1994).

According to the metapopulation concept (Hanski 1991, Ouborg 1993), species can survive in the landscape if their ability to colonise new sites compensates local extinction. Successful colonisation includes both dispersal and establishment and can be affected by both processes (Van der Maarel 1996).

Additionally to the abovementioned limitations site productivity should be taken into account because the relative role of single limiting factors in regulation of species diversity can differ notably along its gradient. This assumption is known as the Shifting Limitations Hypothesis (Foster 2001, Foster et al. 2004) and can be proved by investigating factors limiting species diversity at sites with different productivity.

Finally, seed- and microsite-limitation should be considered with respect to the establishment of populations of single species (population level), and with respect to changes of species diversity at a site (community level; Palmer & van der Maarel 1995).

Though several studies focusing on seed- and microsite-limitation in different ecosystems were performed for different plant species in recent times (e.g. Eriksson & Ehrlén 1992, Hilton & Boyd 1996, Kupferschmidt et al. 2000, Zobel et al. 2000, Overbeck et al. 2003) there is still lack of knowledge about the single processes and their interactions in fen grasslands. This is especially the case, as most mentioned studies regarded either populations of single species or whole communities. In this thesis, results of experiments will be presented and discussed which were performed to study effects of seed- and microsite-limitation on both populations and species richness of fen grasslands. These experiments will additionally contribute to a better understanding of processes, which are necessary for successful fen grassland restoration.

ASPECTS OF GRASSLAND RESTORATION

In general, restoration measures carried out in different types of grasslands with the aim to increase species diversity and preserve populations of rare or endangered plant species can be discussed with respect to the limiting factors for species establishment. In degraded and formerly meso- and oligotrophic wetlands, restoration of site hydrology (e.g. by rewetting) and the reduction of soil nutrients aim to create appropriate abiotic site conditions

for the establishment of target species (of e.g. wet grasslands on clay: Oomes 1999; fen meadows: Jansen et al. 2000, Tallowin & Smith 2001; wet heathlands: Jansen et al. 2004). Disturbance, removal of competitors (via grazing or mowing: e.g. Bakker 1989, Oppermann & Luick 1999, Pykälä 2000) and herbivores (e.g. rabbits: Edwards & Crawley 1999) aim to restore the appropriate biotic site conditions (fen meadow: Overbeck et al. 2003). The creation of safe sites for germination and establishment by e.g. litter removal or creation of patches of bare soil offers new regeneration niches and might abolish microsite-limitation (fen grasslands: Kotorová & Lepš 1999, Overbeck et al. 2003, Poschlod & Biewer 2005).

Further restoration measures, which have become important during the last decades, deal with the abolition of seed-limitation. The cognition, that natural dispersal ability of many plant species is low and insufficient for the colonisation of all appropriate sites in the landscape (e.g. Kotanen 1997), led to the development of measures including transfer and addition of seeds or seed-rich material to restoration areas (e.g. alluvial meadows: Vécrin et al. 2002, Hölzel & Otte 2003; fen grasslands: Patzelt & Pfadenhauer 1998, Cobbaert et al. 2004, Poschlod & Biewer 2005).

In the following, a short overview over some current restoration measures and processes affecting seed- and microsite-limitation in grasslands is given:

Reintroduction of moderate land use (moderate grazing or hay making)

Moderate grazing or cutting for nature conservation is well documented and became a generally accepted method to restore and preserve species-rich grasslands. Numerous studies all over Europe proved the success of these management types for preserving and increasing species diversity (e.g. alluvial grasslands: Ausden et al. 2005; different types of grassland: WallisDeVries et al. 1998; fen meadows: Tallowin & Smith 1996, Hald & Vinther 2000, Stammel et al. 2003, 2004; minerotrophic meadows: Hellström et al. 2003)

The main impact of moderate landuse is to shift the competitive interactions between highly competitive species with a low disturbance tolerance (C-strategists) and weak competitive species with a high disturbance tolerance (S- and R-strategists sensu Grime; Hellström et al. 2003.) Often, the highest species diversity occurs at sites with moderate management intensity, i.e. at intermediate levels of disturbance (intermediate disturbance theory: Connell 1978; e.g. Keddy 2005). Mowing is an important factor reducing the plant biomass and in addition with litter removal increasing the light availability at the soil surface. Grazing livestock reduces vegetation cover by feeding and creates patches of bare soil by trampling. In both cases the number and quality of gaps for germination and establishment increases and thus microsite-limitation is reduced.

A further consequence of long-term site management by mowing and grazing is the reduction of the trophic level of the site by enhancing the biomass output (calcareous grasslands: Willems & van Nieuwstadt 1996; different types of grasslands: Pfadenhauer & Klötzli 1996; grasslands on sandy soils and clay: Berendse et al. 1992). However, the ability of moderate land use to reduce the nutrient level of the soil at a grassland site is strongly dependent on the local conditions to begin of the management and has often been overestimated especially in fen grasslands (Marrs et al. 1989, Güsewell et al. 2000).

In addition, moderate land use might abolish seed limitation, e.g. through the dispersal of seeds by mowing machines (Strykstra et al. 1997) or grazing animals (e.g. Malo & Suarez 1995, Couvreur et al. 2004, Cosyns et al. 2005, Mouissie et al. 2005).

Topsoil removal, sod cutting

In some cases a significant improvement of site conditions at a grassland site solely by means of moderate land use is not possible or takes a very long period of time due to the advanced degradation of the site e.g. as a consequence of drainage or intensive management. An alternative method for such situations is topsoil removal.

The removal of the upper soil horizons in degraded fens causes significant changes by lowering the surface (rewetting) and by the reduction of the nutrient supply down to the level of target community (e.g. alluvial meadows: Hölzel & Otte 2003, Vécrin & Muller 2003; fen meadows: Jansen & Roelofs 1996). Further, topsoil removal and the resulting removal of current vegetation and its seed bank lead to changes of the competitive interactions (e.g. dune slacks: Bakker et al. 2005; fen grasslands: Oomes et al. 1996, Ramseier 2000; forests: De Vries et al. 1995, de Dios et al. 2005; heathlands: Aerts et al. 1995, Verhagen et al. 2001, Allison & Ausden 2004). Finally, large gaps of bare soil occur for further colonisation, which might abolish microsite-limitation (e.g. Patzelt 1998). A successful increase of species diversity after topsoil removal was mainly registered in systems with high natural availability of seeds of target species or when topsoil removal management was accompanied with measures of seed introduction (see below).

Sowing (seed addition, hay transfer)

Sowing (seed mixtures of seeds of single target species), planting and transfer of seed-rich material to abolish dispersal limitation for the purposes of restoration of grassland communities, belong to the praxis of nature conservation in grasslands since the last decades.

These measures appear to be necessary for restoration, because natural dispersal processes are restricted due to a decline of target species plant populations and habitat fragmentation.

In several studies a successful establishment of populations of target species was achieved by the addition of seeds or transplants (fen meadows: Křenová & Lepš 1996; grasslands on former arable soils: McDonald 1993, Lawson et al. 2004, Walker et al. 2004) or the transfer of seed-rich plant material (e.g. alluvial meadows: Hölzel & Otte 2003; fen grasslands: Poschlod & Biewer 2005; minerotrophic meadows: Losvik & Austad 2002).

An important question is the origin of seeds and plant material respectively for transfer. Use of commercial seed mixtures should be seen critically, as especially for the purposes of nature conservation, regionally adapted ecotypes should be preferred (Keller & Kollmann 1998). Hay material harvested in the region fulfill this criteria, but studies dealing with the evaluation of donor sites and analyses of seed content in the plant litter are still rare (but see Biewer & Poschlod 1997).

Additionally, transfer of hay can be seen as measure to reduce microsite-limitation, as in some cases the containing litter material contributes to facilitate germination and establishment of target species, e.g. by protection of seedlings within the litter layer from drought (Eckstein & Donath 2005 in alluvial meadows, Patzelt 1998 in fen meadows). Especially in context with topsoil removal this aspect should not be underestimated.

Although several authors already studied the effects of the single abovementioned measures on vegetation development at restoration sites, a direct comparison of these methods and the effect of their different combinations on the establishment of target species is still lacking. This is especially the case with respect to limiting factors of species diversity in fen grasslands.

RESEARCH QUESTIONS AND OUTLINE OF THE THESIS

This thesis investigates the factors limiting plant populations and species diversity in fen grasslands of Northern Germany and applies measures counteracting the main limitations. For this purposes the response of single (model) species, representing target species of nature conservation and restoration, on seed addition and disturbance as well as transformations of the entire plant community were studied.

The thesis includes results of four discrete investigations (chapters two – five). The first two studies deal with the effects of seed- and microsite-limitation on single species, while the

following two studies discuss the implementation and effects of restoration management on the community level.

Chapter two addresses the question, whether the two endangered fen grassland species *Rhinanthus angustifolius* C.C. Gmel. and *Pedicularis palustris* L. are seed- or microsite-limited at a riparian fen grassland site. Different sowing densities were combined with four types of disturbance in a factorial field experiment to answer this question.

In chapter three, effects of seed- and microsite-limitation on two common fen grassland species were investigated along a gradient in nutrient availability. The two studied species *Silene flos-cuculi* (L.) Clairv. and *Lotus pedunculatus* Cav. both occur within various types of fen-grassland communities differing in standing crop. Thus, they were chosen as model species to answer the question, how fen grassland species differ in their response on seed/plant addition and management (mowing, litter removal) along a productivity gradient.

Chapter four examines the seed content of hay material of different fen grassland sites. It answers the question, if this material could be used for hay transfer to overcome seed limitation of target species at acceptor sites. Further criteria for selecting the most appropriate donor sites for hay transfer are developed.

Chapter five describes a factorial experiment including combinations of three types of restoration measures: hay transfer, moderate (cattle) grazing and topsoil removal. The effects of these measures on different plant species groups and on the establishment success of target species are discussed.

Seed- and microsite-limitation in the fen-grassland species *Pedicularis palustris* and *Rhinanthus angustifolius*

INTRODUCTION

The occurrence of plant species at specific sites is a result of interactions of the regional species pool with colonisation and extinction processes (Eriksson 1993, Tofts & Silvertown 2002). The regional species pool can be defined as a set of species in a certain region, which are theoretically capable of coexisting at a specific site (Zobel 1997). According to Oostermeijer (2003) threats to persistence of (rare) plant species, and thus possible triggers of extinction processes, include environmental factors (e.g. climate change, habitat fragmentation), disturbed biotic interactions (e.g. pollen limitation, herbivory, competition) and genetic factors (e.g. genetic drift, inbreeding). Colonisation is mainly determined by the availability of suitable microsites for germination and establishment (Zobel et al. 2000) and by seed availability, which, in turn, is influenced by seed production, viability and longevity (e.g. Bekker et al. 1998) as well as by dispersal modes and effectiveness (Matlack 2005, Ozinga et al. 2005).

For plant species, existing as metapopulations in the landscape, it is essential to be able to reach new, suitable sites before becoming extinct at the original sites due to habitat alteration, succession, fragmentation or stochastic events (Primack & Miao 1992). Especially for many short-lived species reproducing mainly by seeds, gaps for colonization are thought to be important components of their regeneration niche *sensu* Grubb (1977). In addition, the quality and spatial and temporal distribution of gaps affect species recruitment (Kotanen 1997, Hitchmough 2003). However, the lack of viable seeds in the soil seed bank and of effective dispersal modes may make even suitable sites inaccessible for colonisation by certain species (Bakker et al. 1996).

Whether single plant populations and species richness of plant communities are either seed- or microsite-limited is a question that has received increasing attention during recent years (e.g. Eriksson & Ehrlén 1992, Ehrlén & Eriksson 1996, Hilton & Boyd 1996, Kupferschmidt et al. 2000, Zobel et al. 2000, Overbeck et al. 2003). It is of great importance, both in ecological theory (e.g. for understanding changes in biodiversity; Eriksson & Ehrlén 1992, Zobel et al. 2000) and in practice, especially for the conservation and restoration management of endangered species and communities (Coulson et al. 2001, Pywell et al. 2002).

In Europe, traditionally managed wet grasslands are one of the most species-rich habitat types. Due to changes in agricultural land-use (i.e. in disturbance regime), these wet grasslands have declined both in area and in species diversity during recent decades (Joyce & Wade 1998). In addition, the remnant wet grasslands are highly isolated in the landscape today (Hooftman et al. 2003, Lienert & Fischer 2003) and dispersal between these patches is reduced (e. g. Prach et al. 1996). In general, there is contrasting evidence regarding both seed longevity and seed dispersal ability of wet grassland species (rather low longevity and dispersal capacity: McDonald et al. 1996, Thompson et al. 1997; high longevity and dispersal capacity: Jensen 2004, Soons et al. 2004). Thus, knowledge on effects of different disturbance regimes and of seed availability on the occurrence of habitat-specific wet grassland species is urgently needed to improve the efficiency of nature conservation and restoration practices.

We used the two short-lived hemiparasitic species *Pedicularis palustris* and *Rhinanthus angustifolius* as model organisms in our study to investigate whether microsite- or seed-limitation restricts their populations in wet grasslands and whether their population dynamics is regulated by density dependent (positive or negative) intraspecific interactions. Short-lived hemiparasites are especially suited for the study of colonisation and extinction processes in grasslands. They are non-perennial species without clonal reproduction, able to develop in dense vegetation due to the parasitic interactions with the host plants, but they might also suffer from light competition with the same hosts (Matthies 1995). Thus, they are particularly sensitive to changes in their environment (Ter Borg 1985, Matthies 1991). We carried out a factorial field experiment combining varying seed-sowing densities with different disturbance treatments to answer the following specific questions:

- i. How does microsite availability affect seedling recruitment, establishment and reproduction of *Pedicularis palustris* and *Rhinanthus angustifolius*?
- ii. How does sowing density affect seedling recruitment, establishment and reproduction of *Pedicularis palustris* and *Rhinanthus angustifolius*?

- iii. Are the population dynamics of the species affected by (positive or negative) density-dependent interactions?
- iv. What are the consequences for the conservation of *Pedicularis* and *Rhinanthus* populations or their reestablishment after local extinction?

METHODS

Study species

Both species studied, *Rhinanthus angustifolius* C.C. Gmel. and *Pedicularis palustris* L., hereafter referred to by their genus name, belong to *Orobanchaceae* (formerly *Scrophulariaceae*, tribe of *Rhinanthoidea*) and are, like almost all species of this tribe, non-host-specific hemiparasitic herbs. In Northern Germany, both species were quite common in fen grasslands in the past, but they have become rare due to changes in land-use during recent decades (Jensen & Schrautzer 1999).

Pedicularis palustris L. ssp. *palustris* is a mainly biennial monocarpic species, reproducing only via seeds. It occurs in natural fens and semi-natural fen grasslands. Seeds of *Pedicularis* germinate mainly in spring after cold stratification, but some germination occurs also in late summer directly after shedding. Seedlings recruited in spring exhibit a biennial life-cycle: They form a rosette in the first growing season, overwinter as a winterbud and flower in June–July of the second season. Seedlings recruiting in late summer finish their life-cycle within one year; that is, they behave as annuals (Ter Borg et al. 1980, Karrenberg et al. 2000). The seeds of *Pedicularis* can survive in the soil for more than five years; thus, the species is able to build up a long-term persistent seed bank (Jensen 2004). The seeds have an average mass of 1.1 mg and are buoyant; hydrochory is considered to be the main dispersal mode of this species (Kleinschmidt & Rosenthal 1995).

Rhinanthus angustifolius C. C. Gmel. is an annual that occurs in different types of grasslands, but is most typically found in hay meadows. The species is promoted by mowing: It develops ecotypes adapted to the mowing date (Ter Borg 1972) and has been found to be dispersed by mowing machines (Strykstra et al. 1996). The seeds need a chilling period in order to break dormancy (Pons 1991). Although *Rhinanthus* is known to be able to build up a short-term persistent seed bank (Fürst 1931, Jensen 2004), it strongly depends on the annual seed input. Fluctuations in population size and density related to the seed rain of the previous season have been observed in some cases (Rabotnov 1959, De Hullu et al. 1985). The average seed mass is 2.2 mg. Seed shape is oblate with wings, which can be interpreted as an adaptation to wind dispersal (Bullock et al. 2003).

Study site

The study site is a mesotrophic fen grassland within a kettle-hole mire at the periphery of the Upper Eider valley near Kiel in Northern Germany (54°13'41" N, 10°01'43" E.). The area is moderately grazed since 1999. The vegetation is dominated by herbs (e.g. *Geum rivale*, *Caltha palustris*, *Lythrum salicaria*), grasses (*Poa trivialis*, *Holcus lanatus*) and low-growing sedges (*Carex nigra*). The groundwater level, which was regularly measured within the experimental area during summer 2002 and 2003, was between 8 and 2 cm below soil surface on average. The study site is hydrological separated from the floodplain of the river Eider and thus can not be flooded by river water. Lateral groundwater flux is the most important hydrological pathway of the study site. Neither *Pedicularis* nor *Rhinanthus* occurred at the study site prior to the experiment. The closest known natural population of *Rhinanthus angustifolius* was several hundred metres distant and that of *Pedicularis palustris* several kilometres away from the study site. Thus, colonisation by natural dispersal is unlikely.

Field experiment

We used a nested split-plot design with ten blocks (replicates) à one m² for each of the two species separately. Within each block, each treatment combination of four sowing densities (unsown control, 10, 50 and 200 seeds per subplot; i.e. 250, 1250 and 5000 seeds per m²) and four disturbance treatments (control, mowing, small gaps and large gaps) was applied once, in December 2001. We divided the blocks into four 0.5 x 0.5 plots to which we randomly applied the disturbance treatments: Small gaps were created by removing 50% of the turf in 5 x 5 cm pieces, large gaps by cutting out the entire turf from the plot and mowing was carried out by removing the standing crop. Furthermore, each plot was divided into four 0.2 m x 0.2 m subplots, each surrounded by a buffer strip of 2.5 cm. Within these subplots, seed availability was manipulated by the sowing treatments (Fig. 1).

The seeds were collected in summer 2001 on a species-rich fen grassland (Lehmkuhlener Stauung, 54°12'18" N, 10°20'19" E), approximately 20 km away from the study site, where large populations of both species occurred. The collected seeds were dried and stored at room temperature until sowing, which took place in December 2001 in order to ensure seed stratification under natural temperature and moisture conditions during winter.

The number of individuals per subplot was registered five times for both species and in all treatment combinations: for *Pedicularis* on 27th of May, 18th of June, 6st and 27th of July 2002 and 23rd of June 2003; for *Rhinanthus* on 9th and 27th of May, 18th of June, 6st and 27th of July 2002. The number of individuals occurring on the plots in May 2002 was used as a measure of seedling recruitment and the number of individuals present in July 2002 was

treated as a measure of establishment success. In order to analyse seedling survival, we counted the number of individuals present in July 2002 and calculated the value of survived individuals in relation to the number of seeds sown. In addition, the number of seedlings present in May in relation to the number of seeds sown was counted and calculated to test whether the recruitment percentage was influenced by sowing density and disturbance.

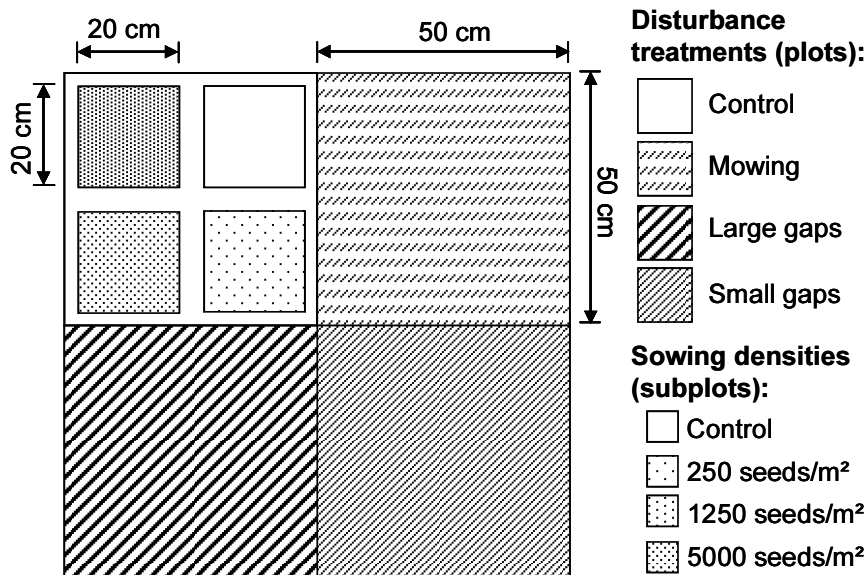


Figure 1. Experimental design of the two-factorial field experiment: One block of ten per species with the combination of the used disturbance treatments “control”, “mowing”, “small gaps” and “large gaps” and sowing densities of 250, 1250 and 5000 seeds/m² and an unsown control is shown.

The reproductive output of the species studied was estimated by counting the fruit capsules produced per subplot of *Rhinanthus* during summer 2002 and of *Pedicularis* during summer 2003.

In summer 2003, the number of generative *Rhinanthus* individuals of the second generation was counted for each block. The effects of the treatment combinations could no longer be distinguished, as seeds had been dispersed between the plots within each block.

Data analysis

A Repeated Measurements ANOVA was used to analyse the effects of microsite- and seed-limitation on the temporal change in the number of individuals during the period of investigation. In this analysis, we only included the first four registration dates for each species as only these dates were equidistant. Time was considered as an inter-group factor in the ANOVA model. Effects of disturbance were tested against the residual variation among

plots, those of sowing density and of the disturbance-by-sowing-density interaction against the residual variation among subplots, and those of time and all interactions with time against the residual. Seedling recruitment, establishment success and reproductive output of the species studied were each analysed separately by a Three-way ANOVA to test the interactive effects of sowing density, disturbance and the blocking factor. Disturbance and sowing density were handled as fixed and block as random factor. Furthermore, a Three-way ANOVA was calculated to analyse the effects of block, disturbance and sowing density on recruitment percentage and seedlings survival of both species. In all these analyses the unsown control was excluded. Only a very few seedlings occurred in unsown subplots, so that the large number of zero values caused extraordinary problems with the ANOVA assumptions.

All data except recruitment percentage and seedling survival were $\log_{10}(x+1)$ transformed to improve normality and the homogeneity of variances. The homogeneity of variances was tested using Cochran tests. Tukey's HSD-tests (multiple comparisons in pairs) were used to analyse the differences between the various levels of the factors (block, sowing density and disturbance). All statistical analyses were carried out with Statistica 6.0 in which the General Linear Model (GLM) procedure was used to specify the syntax of the statistical analyses in relation to the experimental design used. The treatment effects and mean square ratios used in the ANOVA model are presented in Tables 1 to 4.

RESULTS

The overall effects of disturbance, sowing density, time and block on the number of individuals (Repeated Measurements ANOVA) are presented in Table 1. Disturbance had a significant effect on the number of individuals occurring of *Pedicularis*, but not of *Rhinanthus*. Sowing density had a significant effect on the number of individuals of both species. The blocking factor significantly affected the number of individuals of *Rhinanthus*, but not of *Pedicularis* (Tab. 1). For both species, the number of individuals declined significantly during the investigation period. For *Pedicularis*, the reduction of the individual numbers during the time was dependent on disturbance and sowing density, while for *Rhinanthus* no interactions between time and disturbance or time and sowing density could be observed.

Seedling recruitment

In all, 904 seedlings of *Pedicularis* and 1340 seedlings of *Rhinanthus* emerged on the experimental plots in May 2002. Seedling recruitment of both *Pedicularis* and *Rhinanthus*

was significantly affected by sowing density (Tab. 2, Fig. 2 A, B) but only *Pedicularis* was affected by disturbance (Tab. 2; Three-way ANOVA).

Table 1. Effects of block, disturbance, sowing density and time on the number of individuals of *Rhinanthus angustifolius* and *Pedicularis palustris* occurring on the experimental plots during summer 2002. In the mixed model ANOVA block was treated as a random factor. Disturbance, sowing and time were treated as fixed factors. **: $p < 0.01$, ***: $p < 0.001$.

Source of variation	df	Effect MS / Error MS	<i>Rhinanthus</i>			<i>Pedicularis</i>		
			MS	F	p	MS	F	p
Block [B]	random	9	3.0824	2.6	**	1.0690	2.1	ns
Disturbance [D]	fixed	3 D / (B x D)	1.5303	9.0	ns	9.6250	32.5	***
Plot [B x D]	random	27	0.8200	2.0	***	0.2957		
Sowing density [S]	fixed	2 S / (B x S) + (B x S x D)	23.3676	89.8	***	14.0067	67.4	***
D x S	fixed	6 D x S / (B x S) + (B x S x D)	0.2039	0.8	**	0.6591	3.2	**
Subplot [(B x S) + (B x S x D)]	random	72	0.2603			0.20775		
Time [T]	fixed	3 T / R	0.2592	108.0	**	1.8638	59.1	***
T x D	fixed	9 T x D / R	0.0272	36.0	ns	0.1038	3.3	***
T x S	fixed	6 T x S / R	0.0357	54.0	ns	0.3244	10.3	***
T x D x S	fixed	18 T x S x D / R	0.0252	18.0	ns	0.0666	2.1	**
Residual		324	0.0625			0.0315		

The recruitment of *Pedicularis* was significantly higher in all disturbance treatments than in the control (Tukey's HSD: $p < 0.001$ between control and each disturbance treatment). However, no significant differences were found between the disturbance treatments "mowing" and "small gaps" but between "mowing" and "large gaps" (higher recruitment in plots with large gaps, Tukey's HSD: $p < 0.05$; Fig. 2 B). In *Rhinanthus*, the number of seedlings only differed slightly (non significant) between the mown plots (highest recruitment) and large gaps (lowest recruitment).

Table 2. Effects of block, disturbance and sowing density on the number of individuals of *Rhinanthus angustifolius* and *Pedicularis palustris* occurring on the experimental plots in May 2002 (seedling recruitment) and in July 2002 (establishment success). In the Mixed Model ANOVA block was treated as a random factor. Disturbance and sowing density were treated as fixed factors. **: $p < 0.01$, ***: $p < 0.001$.

Source of variation	df	Effect MS / Error MS	<i>Rhinanthus</i>						<i>Pedicularis</i>					
			May			July			May			July		
			MS	F	p	MS	F	p	MS	F	p	MS	F	p
Block [B]	random	9	1.0138	11.2	***	0.5880	8.5	***	0.2619	4.0	***	0.3062	4.8	***
Disturbance [D]	fixed	3 D / (B x D)	0.5665	2.5	ns	0.3668	2.1	ns	2.1045	15.7	***	2.4964	32.7	***
Plot [B x D]	random	27	0.2243			0.1783			0.1344			0.0764		
Sowing density [S]	fixed	2 S / R	7.1214	78.6	***	5.4319	79.0	***	6.2302	96.0	***	1.5094	23.6	***
D x S	fixed	6 D x S / R	0.0643	0.7	ns	0.0876	1.3	ns	0.2131	3.3	**	0.2533	4.0	**
Residual		72	0.0906			0.0688			0.0649			0.0639		

Establishment success

In *Pedicularis*, 377 individuals (41.7 % of the seedlings recruited in May 2002) had established until July 2002. Establishment success was significantly affected by sowing density and by disturbance (Tab. 2; Three-way ANOVA). The “large gaps” and “small gaps” treatments had significantly higher establishment than the “mowing” and control treatments (Tukey's HSD: $p < 0.001$; Fig. 2 C).

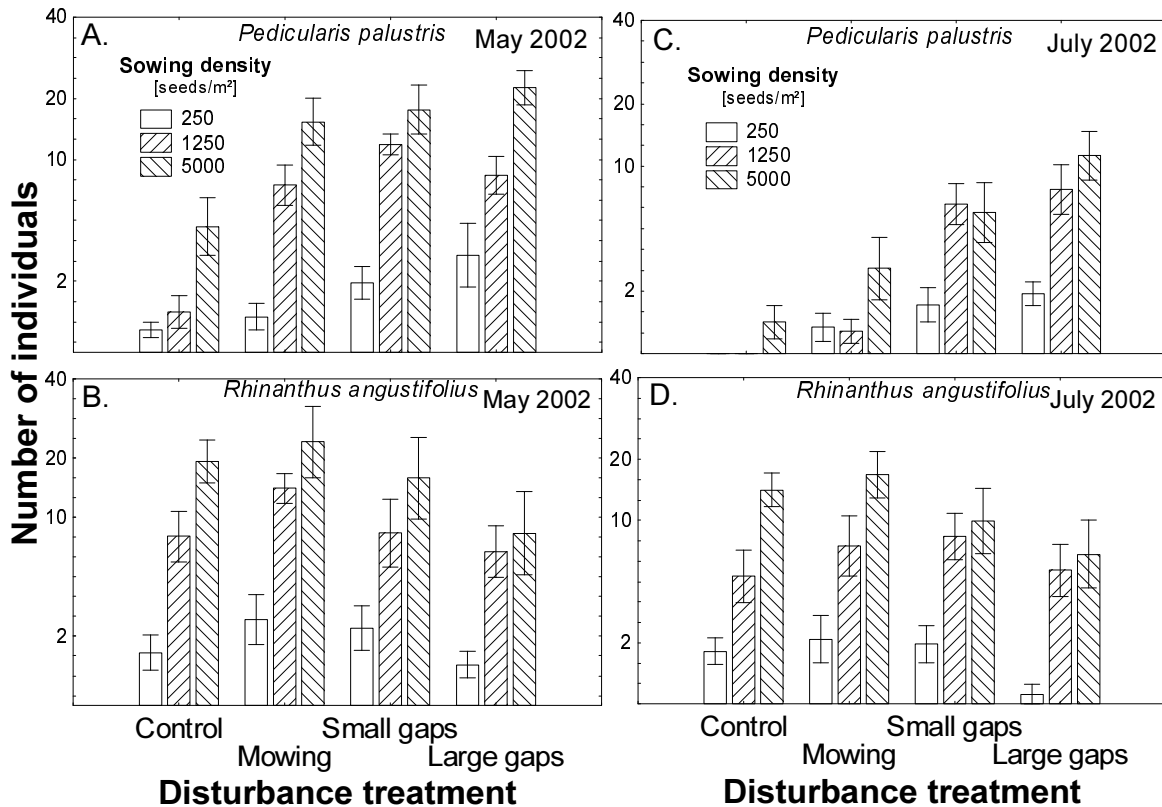


Figure 2. The influence of four different disturbance treatments and three sowing densities on seedling recruitment (number of individuals in May 2002) of *Pedicularis palustris* (A) and *Rhinanthus angustifolius* (B) and on establishment success (number of individuals in July 2002) of *Pedicularis palustris* (C) and *Rhinanthus angustifolius* (D). Mean \pm standard error are presented.

In *Rhinanthus*, 792 individuals (59% of the seedlings recruited in May 2002) had established until July 2002. Establishment success was significantly affected by sowing density (Tab. 2, Three-way ANOVA) but not by disturbance. The “large gaps” treatment led to slightly lower establishment than the “mowing” and “small gaps” treatments (Fig. 2 D).

Seedling survival

In July 2002, a significantly lower seedling survival was observed for both species on the subplots with the highest sowing density (5000 seeds per m²) compared to the other sowing densities (for *Pedicularis*: Tukey's HSD test: $p < 0.05$ between sowing density 250 and 5000 seeds/m² as well as between 1250 and 5000 seeds/m²; for *Rhinanthus*: Tukey's HSD test: $p < 0.05$ between sowing density 250 and 5000 seeds/m² and $p < 0.01$ between 1250 and 5000 seeds/m²). In contrast, the recruitment percentage in May 2002 did not differ significantly between the sowing density treatments for *Pedicularis* while for *Rhinanthus* a difference between the recruitment percentage between the highest and the intermediate sowing density was observed (Tab. 3; Tukey's HSD test: $p < 0.05$ between sowing density 1250 and 5000 seeds/m²).

Table 3. Effects of block, disturbance and sowing density on the recruitment and survival percentage (to the number of sown seeds) of *Rhinanthus angustifolius* and *Pedicularis palustris*. In the Mixed Model ANOVA block was treated as a random factor. Disturbance and sowing density were treated as fixed factors. *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

Source of variation	df	Effect MS / Error MS	<i>Rhinanthus</i>						<i>Pedicularis</i>					
			% recruitment			% survival			% recruitment			% survival		
			MS	F	p	MS	F	p	MS	F	p	MS	F	p
Block [B]	random	9	1179.93	2.8	*	468.74	2.7	*	342.34	1.2	ns	112.86	2.5	*
Disturbance [D]	fixed	3 D / (B x D)	905.06	2.1	ns	423.18	2.4	ns	1455.47	5.0	**	659.23	14.6	***
Plot [B x D]	random	27	421.46	3.1		175.68	2.1		292.10	2.3		45.27	1.4	
Sowing density [S]	fixed	2 S / R	531.26	3.9	*	517.68	6.1	**	290.10	2.3	ns	187.60	5.7	**
D x S	fixed	6 D x S / R	86.47	0.6	ns	96.01	1.1	ns	377.41	3.0	*	74.63	2.3	*
Residual		72	136.20			84.33			126.67			32.94		

Reproductive output

In *Pedicularis*, fruit production per subplot was significantly affected by sowing density and by disturbance (Tab. 4, Three-way ANOVA). The reproductive output on plots without disturbance and on mown plots was lower than on plots with gaps (Tukey's HSD test: $p < 0.01$). The difference between plots with small and large gaps was not significant (Fig. 3 A). Furthermore, fruit production increased with sowing density.

Fruit production of *Rhinanthus* per subplot was significantly affected by sowing density (Tab. 4; Three-way ANOVA), but not by disturbance (Fig. 3 B). Fruit production was significantly lower on the subplots with the lowest sowing density (250 seeds/m²) than on the plots with sowing densities of 1250 and 5000 seeds/m² (Tukey's HSD test: $p < 0.001$), but there were no significant differences between the two higher sowing densities. In all, 1239

flowering individuals of the second generation were observed at the study site in summer 2003 (compared to 792 generative individuals in 2002).

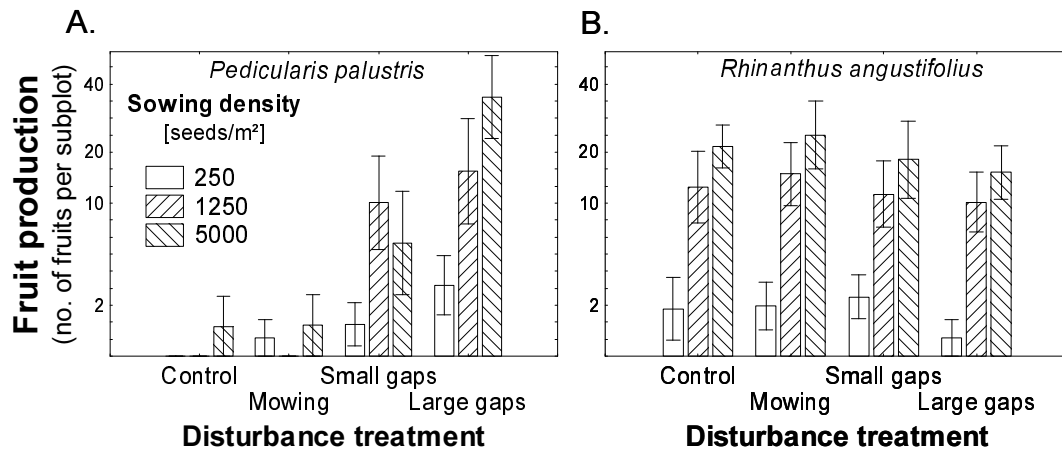


Figure 3. Reproductive output (number of fruit capsules) of *Pedicularis palustris* (A) and *Rhinanthus angustifolius* (B) at four different disturbance treatments and three sowing densities in the summers of 2002 (*Rhinanthus*) and 2003 (*Pedicularis*). Mean \pm standard error are presented.

DISCUSSION

Seed limitation and density-dependent effects on survival and reproduction

By experimental seed addition, effects of seed limitation have been demonstrated for many species during recent years (e.g. Eriksson & Ehrlén 1992, Tilman 1997). In most cases seed addition led to the establishment of new populations of the species sown (Stampfli & Zeiter 1999, Foster & Tilman 2003) or, if the species already occurred, to an increase of population density (Zobel et al. 2000). Thus, seed limitation is an important factor for population dynamics in many species. Nevertheless, Gustafsson & Ehrlén (2002) showed that *Sanicula europaea* was not seed limited.

In the present study, seed addition resulted in the occurrence of seedlings of both *Pedicularis* and *Rhinanthus*. In addition, a large number of flowering individuals of *Rhinanthus* of the second generation occurred at the study site in summer 2003. These results are in accordance with most of the aforementioned studies and show that the establishment was successful after the absence of viable seeds had been overcome by sowing. This demonstrates that the site conditions of the mesotrophic fen site (Calthion) with a high groundwater level and some members of the *Comarum* species-group present (e.g. *Potentilla palustris* and *Carex canescens*) were suitable for both species. Recruitment from the seed bank or after natural dispersal is very unlikely to have taken place, as neither

species was present in the vegetation of the study site and the surrounding area during recent years (Jensen, pers. observ.).

Table 4. Effects of block, disturbance and sowing density on the fruit production of *Rhinanthus angustifolius* and *Pedicularis palustris* occurring on the experimental plots in summer 2002 (*Rhinanthus*) and in summer 2003 (*Pedicularis*). In the Mixed Model ANOVA block was treated as a random factor. Disturbance and sowing density were treated as fixed factors. *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

Source of variation	df	Effect MS / Error MS	<i>Rhinanthus</i>			<i>Pedicularis</i>		
			MS	F	p	MS	F	p
Block [B]	random	9	1.4902	9.3	***	0.8052	2.7	**
Disturbance [D]	fixed	3 D / (B x D)	0.1931	0.7	ns	6.0916	14.7	**
Plot [B x D]	random	27	0.2775			0.4151		
Sowing density [S]	fixed	2 S / R	9.6167	60.1	***	2.1986	7.4	**
D x S	fixed	6 D x S / R	0.0270	0.2	ns	0.8004	2.7	*
Residual		72	0.1601			0.2968		

As the number of recruiting seedlings increased with sowing density, occurrence of both species was seed-limited over the range of the sowing densities applied (see also Parker 2001). However, seedling survival on the plots with the highest sowing density was lower than at the other sowing densities – probably as a consequence of intraspecific competition between seedlings. For monocarpic species with low dispersal ability it has previously been shown that mortality in the early growth stages (rosettes, seedlings, juvenile plants) is often dependent on local population density, while site conditions play a major role in survival and growth of later growth stages (flowering and fruit production; e.g. Juenger & Bergelson 2000, Suzuki et al. 2003). In previous studies, negative density-dependent effects on seedling survival had been observed in both *Pedicularis palustris* (Jensen, unpublished) and *Rhinanthus angustifolius* (at seedling densities over 1000 per m²; Ter Borg 1979). Also, Van Hulst et al. (1987) mentioned increasing mortality for the related species *Rhinanthus minor* at high population densities. In contrast to these results, Matthies (2003) reported positive interactions among seedlings of the related species *Rhinanthus alectorolophus* in early stages of recruitment leading to lower mortality at high sowing densities of 1600 per m² and negative density dependent effects only in later stages of the life cycle (growth, reproduction).

An alternative explanation for the phenomenon that population density approaches saturation with increasing sowing density is that seed limitation is replaced by microsite-limitation at high sowing densities as all suitable microsites for germination and establishment become occupied (see Harper 1977).

Microsite-limitation and disturbance regime

In accordance with ecological theory (Eriksson & Ehrlén, 1992), *Pedicularis* was microsite-limited in the present study, as the number of individuals in the undisturbed control plots was significantly lower than in plots with disturbance, even at the highest sowing density. Also the reduction of individuals in the course of time was dependent on disturbance treatments. Thus, the presence of gaps was an important prerequisite for the establishment of this species. Positive effects of gaps were also mentioned for other wet grassland species (Spackova et al. 1998, Overbeck et al. 2003). In contrast, seedling recruitment of *Rhinanthus* was not affected by disturbance, which indicates that this species was not microsite-limited. This is in concordance with De Hullu (1985) who also showed that *Rhinanthus angustifolius* does not depend on created gaps even at rather high population densities. Also, large gaps might even decrease the reproductive output of root-hemiparasites due to the lack of available host plants (De Hullu, 1985), but this effect was not observed in our study. In agreement with our results on *Rhinanthus angustifolius*, Coulson et al. (2001) only found minor effects of management regime on seedling recruitment and survival of *Rhinanthus minor*. Some other related hemiparasitic species are known to develop highest population densities under intermediate disturbance conditions (e.g. *Euphrasia frigida*, Nyléhn & Totland 1999).

In general, *Rhinanthus* occurs within a wide range of plant communities with various nutrient and moisture conditions (Fürst 1931), while *Pedicularis* strongly depends on wet and oligotrophic site conditions (Rosenthal & Fink 1996). The ability of this species to persist on moderately-used mesotrophic fen grasslands as secondary habitats can be seen as a consequence of a reduction in light competition caused by grazing or mowing (e.g. Bakker 1989) and by the creation of suitable microsites for germination and establishment. The abandonment of former moderately-used fen grasslands often leads to increased litter accumulation, a lack of gaps and an increase in standing crop and light competition, which in turn leads to a decline and often the local extinction of *Pedicularis* populations after abandonment (Jensen & Schrautzer 1999). Germination of larger-seeded species like *Rhinanthus* is less hampered by thick litter layers (Jensen & Gutekunst 2003) and, thus, these species are less affected by abandonment than small-seeded ones.

CONCLUSIONS

Both species studied are regarded as rare or endangered in Northern Germany. In particular, the number of *Pedicularis palustris* populations has declined dramatically during recent decades (Karrenberg et al. 2000). Due to its habitat demands, *Pedicularis* can be

considered to be a fugitive biennial (Van der Meijden et al. 1992) that is dependent on patches of bare soil for germination and seedling establishment. This must be taken into account when considering the conservation management of its remnant regional populations and restoration management via sowing after its local extinction.

It can be concluded that the two species studied differ in their reaction to disturbance treatments, as disturbance influenced the availability of microsites for them in a different way: the larger seeded *Rhinanthus* was able to establish populations after sowing independent of disturbance and thus was not microsite-limited, while *Pedicularis* (a weak competitor with smaller seeds) needed gaps for germination and establishment and thus was microsite-limited. Additionally, both species were seed-limited, as higher sowing densities resulted in higher numbers of plants in all treatments. Additionally it could be shown, that seed densities of 5000 seeds per m² approached the saturation and it can be recommended to the purpose of reintroduction of the species in the landscape not to exceed this value.

Plate I



Picture 1. Experimental plot of the two-factorial field experiment with different disturbance treatments: control, large gaps, mowing, small gaps (treatments are highlighted with a dotted line; December 2002).



Picture 2. Site of the two-factorial field experiment with flowering *Rhinantus angustifolius* C.C. Gmel. individuals in June 2003.

Effects of litter removal and mowing on germination and establishment of two fen-grassland species along a productivity gradient

INTRODUCTION

Knowledge about the reasons and mechanisms of biodiversity losses in fen grasslands is the first step on the way to the successful management of still existing species-rich grassland sites and the reintroduction of endangered wetland species. Mineralization and associated eutrophication of drained fens as well as the abandonment of formerly moderately used fen grassland sites are considered to be the main factors for the disappearance of many formerly common fen grassland species (Wheeler & Shaw 1991, Jensen & Schrautzer 1999). For an understanding of the mechanisms leading to decreased species richness several models including effects of plant litter (e. g. Facelli & Pickett 1991, Xiong & Nilsson 1999, Weltzin et al. 2005), light penetration (Wilson & Tilman 1993), nitrogen availability (Wilson & Tilman 1991, Henry et al. 2004) and above- and belowground biomass (e.g. Twolan-Strutt & Keddy 1996) have been presented in the literature during the last two decades. For most of these studies it can be summarised, that an increase of nutrient availability and a reduction of disturbance in form of grazing or mowing leads to a shift in the competitive interactions between plants. Tall-growing nitrophytic species (c-strategists sensu Grime 1977) become dominant, while weaker competitors disappear due to a lack of available niches for germination and establishment (Tilman 1988). This effect was studied especially at dry grassland prairies or old fields (Wilson & Tilman 1991, Wilson & Tilman, 1993, Foster & Gross 1998, Peltzer et al. 1998, Foster 1999), but also at fen sites (Twolan-Strutt & Keddy 1996). Changes in site conditions in favour of weak competitors can be achieved by the reestablishment of traditional management types like e.g. mowing or moderate grazing (e.g. Rowell et al. 1985, Olf et al. 1999).

In addition to the above mentioned, the availability of propagules is of importance for species occurrence. Long-term experiments showed that after the re-introduction of an appropriate grassland management the soil nutrient status and biomass production has been adapted to the demands of target communities, but an increase of species diversity often failed (Berendse et al. 1992). Habitat fragmentation due to changes in land use hampers the exchange within metapopulations and thus reestablishment after local extinction. In this case dispersal-limitation seems to be the main factor (Primack & Miao 1992, Münzbergová & Herben 2005) and must be overcome by management efforts like transfer of seeds or seed-rich material (Biewer & Poschlod 1997, Hölzel & Otte 2003).

Limitation of niches and dispersal limitation can be thus seen as main factors, explaining species composition. Even though each of these factors is well known, there is still little information about the interaction between them and the response of single species on this interaction. Foster et al. (2004) assumed, that factors limiting species diversity in grasslands shift from seed availability to niche availability with increasing productivity of the site (Shifting Limitation Hypothesis, see also Foster 2001). This theory was tested experimentally in dry prairie grasslands (Foster & Gross 1998, Henry et al. 2004).

In the present study we report the results of a field experiment carried out along a productivity gradient, in which seeds and transplants of two common fen grassland species were added to a factorial arrangement of litter removal and mowing treatments. The treatments were chosen to investigate the separate and interactive effects of living competitors and plant litter on the studied species. Both seeds and transplants were used to examine litter and standing crop effects on germination and initial seedling establishment on the one hand and on biomass of established individuals on the other hand. We assume that a shift from sites with poor to sites with rich soil resources and higher productivity can cause a shift from dispersal- to establishment- limitation and expect different responses of sown and transplanted individuals (Henry et al. 2004) on these factors. Thus, we installed the experiment at seven study sites representing the range of standing crop and soil nutrient content in fen grassland communities available in Northern Germany. The investigated species (*Silene flos-cuculi*, *Lotus pedunculatus*) represent typical plant species of fen grassland communities and are moderately sensitive to land use intensification or abandonment (Schrautzer & Jensen 1999).

The main questions of the study were:

- i) Does growth and survival of *Silene* and *Lotus* differ between and within fen grassland communities of various productivity dependent on the treatments (litter removal, mowing)?

- ii) Does the two studied species differ due to their competitive ability and reaction to litter removal and/or mowing?
- iii) Can the Shifting Limitation Hypothesis be explained by the results of our experiment?

METHODS

Study species

Lotus pedunculatus Cav. [*Lotus uliginosus* Schkuhr] (Fabaceae) – marsh birdsfoot trefoil is a perennial herbaceous species occurring mainly in different types of fen meadows. It is a character species of the Calthion community. It develops 30-90 cm long ascending shoots, which are looping on the surrounding vegetation, and belowground tillers (Hegi 1979). *L. pedunculatus* is pollinated by insects and is self-dispersed. *Lotus* forms nitrogen-fixing nodules in association with *Rhizobium lupini* and thus is more or less independent of the soil nitrogen content. It can be found under both moderately productive and unproductive conditions, but it disappears from heavily disturbed sites. Additionally, *L. pedunculatus* favours sites, where the growth of the dominant species is limited, e.g. by mowing. It is classified as stress-tolerant competitor (Grime et al. 1989).

Silene flos-cuculi (L.) Clairv. [*Lychnis flos-cuculi* L.] (Caryophyllaceae) – ragged robin, cuckoo flower, is a perennial hemicryptophytic species forming a rosette. The species is common on fen meadows and is known to reach a maximum abundance at managed (mown or grazed) sites and in early abandonment stages, but declines after longer periods of abandonment (Schrautzer & Jensen 1999, Chaloupecká & Lepš 2004). Wolf et al. (1984) considered *Silene* to be a weak light competitor. The seeds germinate better at light, so that generative reproduction can be suppressed by thick litter layers (Milberg 1994). Grime et al. (1989) counted *Silene flos-cuculi* to the csr strategy type (ruderal stress-tolerant competitor).

Study sites

The study was carried out at seven sites in the moraine landscape of Northern Germany, representing the various forms of fen-grassland types, known in the region. Three of the study sites (I, II, and III) are situated in a fen area, the “Lehmkuhlener Stauung”, (54°12’N, 10°20’E), the following site (IV) is part of the siltation area of the lake “Vollstedter See” (54°13’N, 9°52’E), while sites V, VI and VII are situated within the Upper Eider valley (54°13’N, 10°2’E). A brief description of vegetation and soil parameters of the study sites is combined in Table 1.

Table 1. Comparison of the experimental sites regarding vegetation type, biomass and soil parameters. Mean \pm std. deviation.

Area Site	Vegetation description	Standing crop (g dry weight/m ²)	pH	Soil nutrient (mg/100g)				Groundwater (cm below ground)	
				NO ₃ -N	NH ₄ -N	PO ₄ -P	K		Mg
I	Fen grassland, dominated by herbs like <i>Menyanthes trifoliata</i> and <i>Potentilla palustris</i> , invaded by <i>Phragmites australis</i> . Regularly mown once a year in late summer. Litter cover up to 10 %; mean vegetation height: 30 cm.	357 \pm 50	6.2	0.053 \pm 0.010	0.052 \pm 0.024	2 \pm 0	3.7 \pm 1.2	13.5 \pm 1.0	-27.1 \pm 16.5
II	Fen grassland, dominated by <i>Carex panicea</i> , <i>Eriophorum angustifolium</i> and <i>Filipendula ulmaria</i> . Regularly mown once a year in late summer. Litter cover up to 15 %; mean vegetation height: 25-30 cm.	380 \pm 25	5.3	0.027 \pm 0.004	0.122 \pm 0.023	1 \pm 0	2 \pm 0	7.2 \pm 0.4	-20.2 \pm 15.8
III	Fen grassland, abandoned since 5 years. Dominated by <i>Filipendula ulmaria</i> , <i>Calamagrostis canescens</i> , <i>Carex panicea</i> and <i>Lysimachia vulgaris</i> . Litter cover up to 20%; mean vegetation height: 45-50 cm.	556 \pm 24	4.9	0.083 \pm 0.029	0.137 \pm 0.005	1.3 \pm 0.6	4 \pm 1	7.7 \pm 0.6	-30.3 \pm 22.1
IV	Abandoned fen grassland, dominated by <i>Calamagrostis canescens</i> , <i>Peucedanum palustre</i> and small sedges, with about 15 % cover of moss (<i>Sphagnum</i> sp.). Litter cover up to 25 %; mean vegetation height: 40 cm.	482 \pm 58	3.9	0.018 \pm 0.014	0.061 \pm 0.031	5 \pm 0	9.3 \pm 1.5	13.9 \pm 1.3	-19.3 \pm 14.3
V	Abandoned fen grassland, dominated by <i>Calamagrostis canescens</i> , <i>Festuca rubra</i> and <i>Ranunculus repens</i> but with an notable amount of mesotrophic species like <i>Viola palustris</i> and <i>Potentilla palustris</i> . Litter cover up to 3 %; mean vegetation height: 50 cm.	555 \pm 90	5.0	0.048 \pm 0.005	0.289 \pm 0.016	3.7 \pm 1.2	4.3 \pm 0.6	4.1 \pm 1.1	-22.7 \pm 13.7
VI	Abandoned fen grassland, dominated by <i>Phalaris arundinacea</i> and <i>Urtica dioica</i> . Litter cover up to 10 %; mean vegetation height: 80 cm.	593 \pm 51	4.7	0.283 \pm 0.040	0.359 \pm 0.036	7.7 \pm 1.2	4.3 \pm 0.6	3.9 \pm 1.1	-35.6 \pm 21.2
VII	Abandoned fen grassland, dominated by <i>Carex acutiformis</i> . Litter cover up to 20 %; mean vegetation	935 \pm 90	5.3	0.023 \pm 0.007	0.218 \pm 0.028	5.5 \pm 0.6	2.3 \pm 0.6	4.1 \pm 0.4	-5.7 \pm 4.5

Experimental design

At each site six experimental blocks of 2 x 4 m were installed, each including four plots á 1 x 2 m (litter removal and mowing, litter removal without mowing, no litter removal and mowing, no litter removal and no mowing; Fig. 1). 1 m broad buffer stripes were left between the blocks. Litter removal was carried out by raking at the start of the experiment in late autumn 2002, while mowing has been applied first mid of June 2003 and has been repeated in June 2004. Seeds of the studied species were sown into marked subplots á 0.25 x 0.25 m (0.0625 m²) buffered within the treatments with an amount of 200 seeds per subplot (3200 seeds per m²).

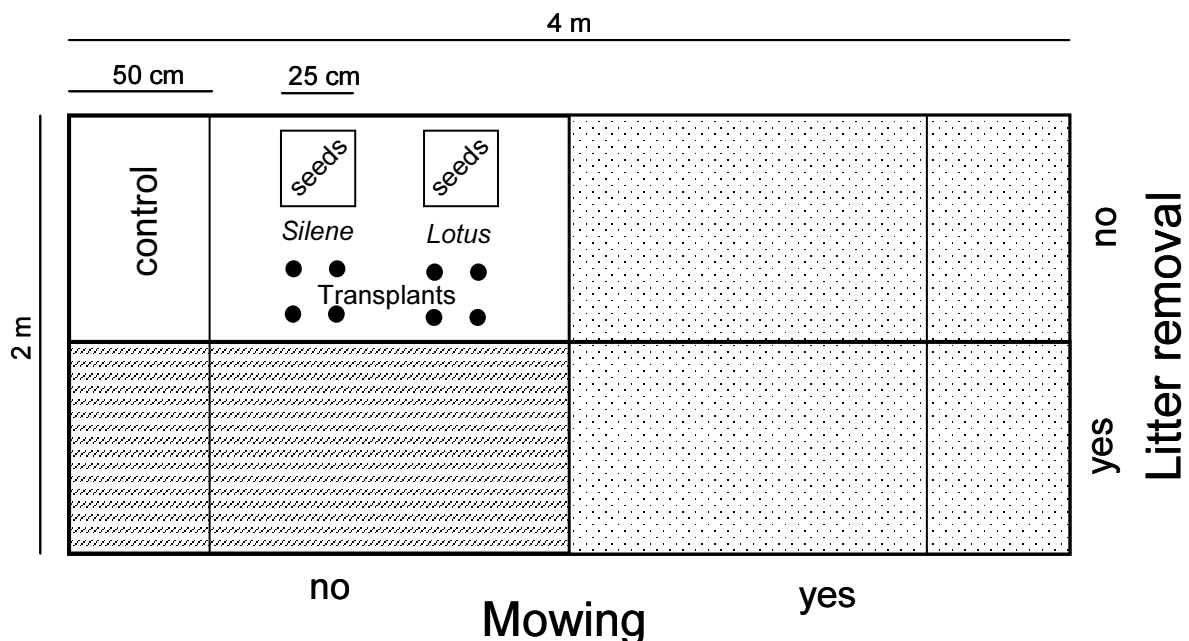


Figure 1. Experimental design illustrating the arrangement of the experimental treatments and the position of transplants and seed addition subplots in each block. One of six blocks in one of seven sites is shown. The experimental treatments are: Litter removal (yes/no), Mowing (yes/no). Sowing density was 200 seeds per subplot (3200 seeds per m²). Four individuals (transplants) of each study species were transferred in every treatment plot.

Sowing was performed by hand directly after litter removal in late autumn 2002 to assure chilling under natural conditions. Seeds of both species were collected in the Upper Eider valley in late summer 2002. Additionally four individuals of each species grown in a greenhouse out of the same seed harvest were transplanted at all experimental sites and treatments in April 2003. Transplants of *Lotus pedunculatus* had a shoot length of about five cm. Transplants of *Silene flos-cuculi* were small rosettes of three-four cm diameter with the first four leaves developed. Within the subplots the transplants were planted with a distance

of 15 cm to each other and marked individually. In each treatment a 1 x 0.5 m large margin was left as unsown and unplanted control, where naturally occurring individuals of the studied species were counted. Naturally established individuals of *Silene flos-cuculi* were only detected at study sites in Lehmkuhlener Stauung (I-III) and of *Lotus pedunculatus* additionally at site V in the Upper Eider Valley, but in each case their density was much lower than in the experimentally sown subplots so that their impact on the experimental results can be neglected. When the sites for the experiment were selected, we avoided areas with larger autochthonous populations of the studied species.

The number of seedlings and survived transplants was registered at the end of summer 2003 and 2004. In August 2004 all individuals occurring on the experimental plots except the control margin were collected, dried at 40°C and weighed.

Standing crop, light and nutrient availability, hydrology

In late June 2003 the maximum standing crop at each study site was determined by harvesting the entire aboveground biomass at five 0.25 m² plots chosen randomly in the surrounding of the experimental blocks. The samples were dried at 40 °C till a constant mass was reached, and weighed.

Light penetration in the vegetation was measured in mid of July 2003 about four weeks after mowing using a SunScan Canopy Analysis System (type SS1, Delta-T Devices Ltd, Cambridge – UK). The probe includes a 1 m light sensitive “wand” containing 64 photodiodes equally spaced along its length and a control sensor. The probe was inserted in the vegetation 15 cm above the soil surface while the control sensor was installed unshaded above the vegetation. Relative radiation was measured as the mean value of photosynthetic active radiation (PAR) in the canopy in relation to the full light above vegetation. This value was considered as light availability for the studied species. Light measurements were performed in all treatment combinations within each block and study site.

Available nitrogen, phosphorus, potassium and magnesium were measured in soil samples of 0-15 cm depth after the VDLUFA A 5.1.1, A 6.1.1 and A 6.1.2 (VDLUFA 1997). C/N ratio was calculated as an additional measure of soil nutrient availability. Three soil samples were taken from each site in August 2005.

Groundwater table for each site was measured every two weeks during the vegetation periods in 2003 and 2004 and once a month in winter.

Data analysis

We applied Generalized Linearised Mixed Models (GLMM) to analyse the effects of sites and treatments on the recruitment of individuals of both studied species during the two years and on the final biomass of seedlings and transplants.

For this purposes the `glmmPQR` function out of the `MASS` library for R was used, which assumes multivariate normal random effects and uses penalized quasi-likelihood estimation (Venables & Ripley 2002). We modelled the responses of the dependent variables with a Poisson distribution with a log link function. Site, litter removal and mowing were treated as fixed factors, while blocks were treated as random. Numbers of individuals per sown subplot and the mean biomass of individuals and transplants occurring within a single subplot were taken as dependent variables. We carried out a standard ANOVA and estimated the minimally adequate models by sequential backwards removal of the non-significant terms based on conditional F-tests of ANOVA terms. The minimal models were considered as followed: The dependent variables “Number of individuals” and “Mean biomass” were tested against the factors Site, Litter removal and Mowing as well as interactions Site/Litter removal, Site/Mowing and Site/Litter removal/Mowing.

Additionally, we used non-parametric tests (Kruskal-Wallis Test, Mann-Whitney U-Test) to compare the effects of treatments on the number and biomass of studied species within the single study sites. The relationship between average biomass of transplants and standing crop of the study sites as well as between standing crop and light penetration in the vegetation were examined by linear regression.

Differences between sites (standing crop, soil nitrogen content) were analysed using one-way ANOVAs and Tukey HSD tests. Differences in light penetration between the plots were analysed by Kruskal-Wallis Test.

The Generalized Linearised Mixed Models were calculated using the statistical program R 2.1.1 (R Development Core Team 2005), while all other calculations were performed with Statistica 6.1 (Statsoft 2004).

RESULTS

Site conditions

Most study sites differed significantly from each other with respect to nitrogen content in the soil (Fig. 2 A). In contrast, only site VII had significantly higher standing crop than the other studied sites (Fig. 2 B). Light availability at 15 cm above soil decreased with increasing standing crop (Fig. 2 C).

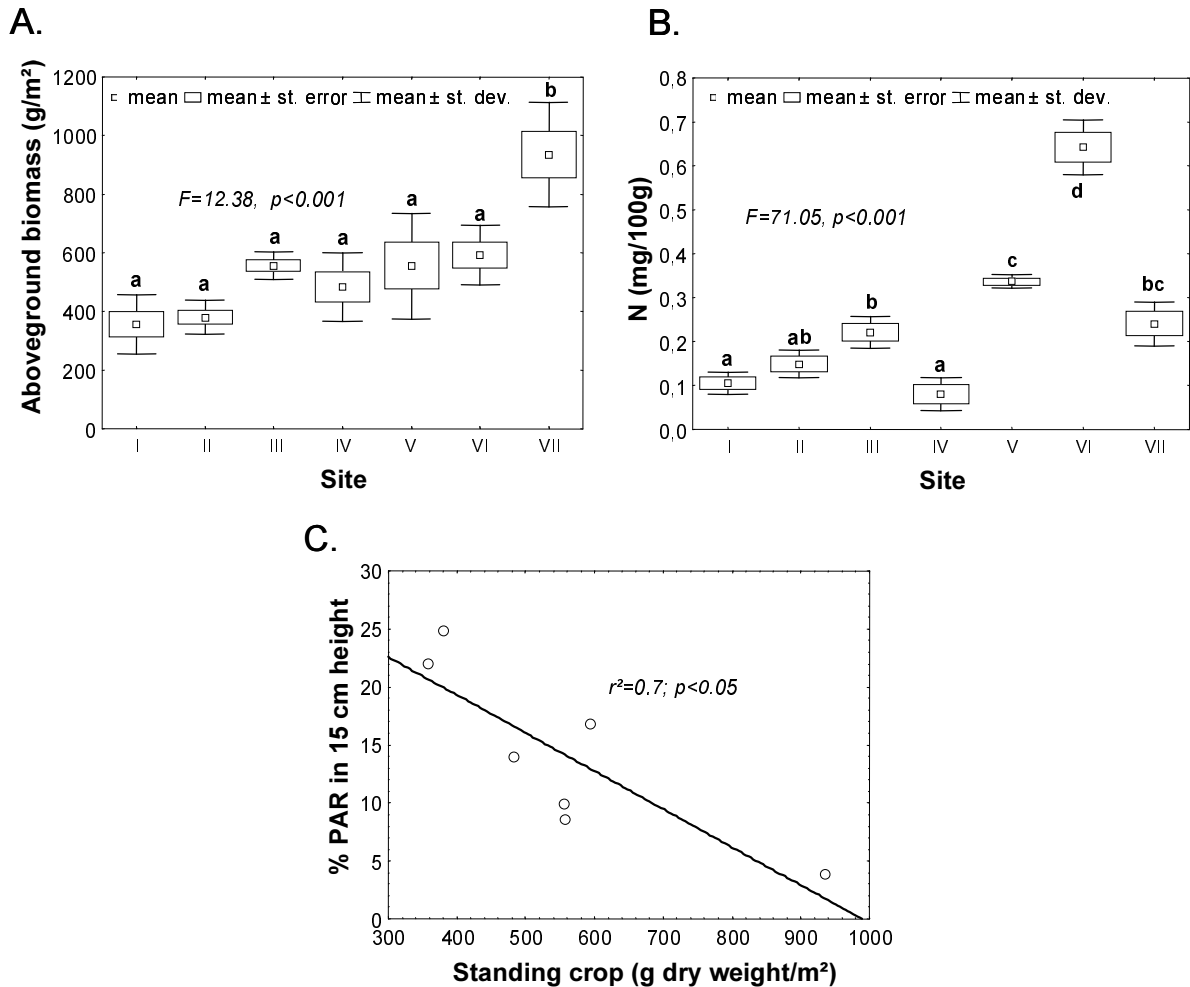


Figure 2. Variety of site conditions along the studied productivity gradient of seven fen grassland sites. **A.** Standing crop, harvested end of June (g. dry weight/m²). **B.** Available nitrogen in the soil (mg/100g, NO₃ and NH₄ counted together). **C.** Relation between standing crop and light penetration in the vegetation of untreated plots in percent Photosynthetic Active Radiation in 15 cm height above the soil surface.

The amount of light at 15 cm above the soil level was significantly higher at mown plots ($H = 49.32, p < 0.001$) and valued between 3 % and 25 % for unmown and 30-50 % for mown plots. This difference was not significant between plots with and without litter removal ($H = 2.05, n.s.$).

Hydrological conditions were similar at all study sites. Groundwater levels averaged between 6 and 36 cm below soil surface, with a minimum of 50-60 cm below soil surface in late summer 2003 during an extraordinary dry period (Tab. 1). No inundation was observed during the time the experiment was performed.

Sowing

The factor site had a significant effect on the recruitment of both studied species after seed addition (Tab. 2).

Table 2. The effects of litter removal and mowing on number and biomass of sown individuals and the biomass of transplants of *Silene flos-cuculi* and *Lotus pedunculatus* analysed at seven sites along a productivity gradient. Standard ANOVA calculated on basis of the final (minimal) GLMM model, * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

	df, den.df	Number of individuals				Biomass of sown individuals		Biomass of transplants	
		2003		2004		F	p	F	p
		F	p	F	p				
<i>Silene flos-cuculi</i>									
Site	6, 135	6.22	***	2.40	*	10.55	***	5.35	***
Litter removal	1, 135	16.65	***	5.54	*	2.87	ns	0.97	ns
Mowing	1, 135	0.02	ns	5.43	*	2.17	ns	1.80	ns
Site / Litter removal	6, 135	0.80	ns	1.25	ns	0.56	ns	1.10	ns
Site / Mowing	6, 135	0.09	ns	1.24	ns	0.94	ns	0.71	ns
Site / Litter removal / Mowing	7, 135	0.16	ns	1.49	ns	0.78	ns	1.70	ns
<i>Lotus pedunculatus</i>									
Site	6, 135	8.84	***	10.13	***	7.26	***	3.99	**
Litter removal	1, 135	28.25	***	3.09	ns	0.14	ns	0.04	ns
Mowing	1, 135	5.45	*	0.22	ns	1.35	ns	0.96	ns
Site / Litter removal	6, 135	1.53	ns	0.69	ns	1.01	ns	0.38	ns
Site / Mowing	6, 135	1.36	ns	1.82	ns	1.44	ns	0.57	ns
Site / Litter removal / Mowing	7, 135	0.35	ns	0.15	ns	0.31	ns	1.10	ns

For all experimental sites taken together litter removal and mowing both led to a significantly higher recruitment of *Lotus pedunculatus* in the first year of the experiment (Tab 2). Within the experimental sites litter removal led to significantly higher numbers of *Lotus* at sites I – IV (with low standing crop; Fig. 3A), while mowing had only a significant effect at site VII (with the highest standing crop; Fig. 3B).

In the second year no effects of litter removal on the number of *Lotus* individuals were observed and the effect of mowing was only present at site VII (Mann-Whitney U-test: $U = 33.5$, $p < 0.05$, results not shown).

For *Silene flos-cuculi* only litter removal led to an increase of the number of individuals out of sown seeds in the first year, while effects both of litter removal and mowing were significant in the second season (Tab. 2). Within the experimental sites, litter removal led to a significant increase of the number of *Silene* individuals only at site IV and VII in the first season (Fig. 4A), while in the second season mowing had the same effects at sites IV and VII (Mann-Whitney-U test, Fig. 4B).

The average biomass of plants per plot, which established after sowing, differed significantly between the sites but not between treatments within the sites (Tab. 2).

Transplants

From the entire number of 672 transplants for each of both studied species 261 transplants of *Silene flos-cuculi* and 279 transplants of *Lotus pedunculatus* survived till the end of the second vegetation period. The survival of transplants differed strongly between the sites. While the survival of both species at sites I to III was about 50 to 60 %, the survival at sites VI and VII amounted to 20-25 % for *Silene* or only to 10 % for *Lotus* at site VI.

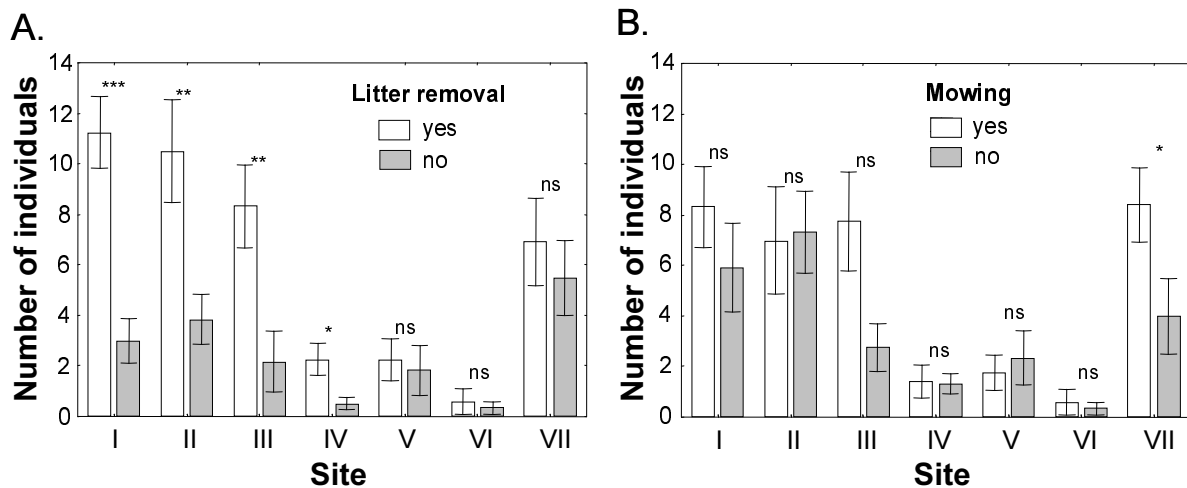


Figure 3. Number of individuals of *Lotus pedunculatus*, recruited out of sown seeds. **A.** - related to factor “Litter” in the first season. **B.** - related to factor “mowing” in the first season. Significances of Mann-Whitney U-test are given as followed: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$. Mean and standard error are shown.

Biomass of transplants of *Silene* and *Lotus* differed significantly between sites, but not between the treatments (Tab. 2). A significant positive relation between standing crop and transplant biomass was observed for *Silene*, but not for *Lotus* (Fig. 5).

The highest biomass of transplants was observed for both species at sites VI and VII (both sites with high nutrient content in the soil). Transplants of *Silene* on mown plots at sites I, IV and VII had a significantly higher biomass than on unmown plots. The same effect was observed for *Lotus* transplants at sites IV and VII. The effects of litter removal were less important for transplant biomass of both species. Only at site VII the transplants of *Silene* were significantly ($U = 66.0$, $p < 0.05$) larger in plots without litter removal than in plots with litter removal (results not shown).

DISCUSSION

In general, species with a low competitive ability are restricted to sites with a low amount of plant litter and standing crop (Al Mufti et al. 1977). Our study species can be seen as

intermediate competitors as they were also able to germinate and establish at sites with high standing crop. Nevertheless, the factor site was still important for the successful recruitment. Especially at less productive sites the number of individuals established after sowing could be additionally increased by removing plant litter. We conclude that this effect is a consequence of an increasing number of available gaps for germination at sites with lower vegetation density.

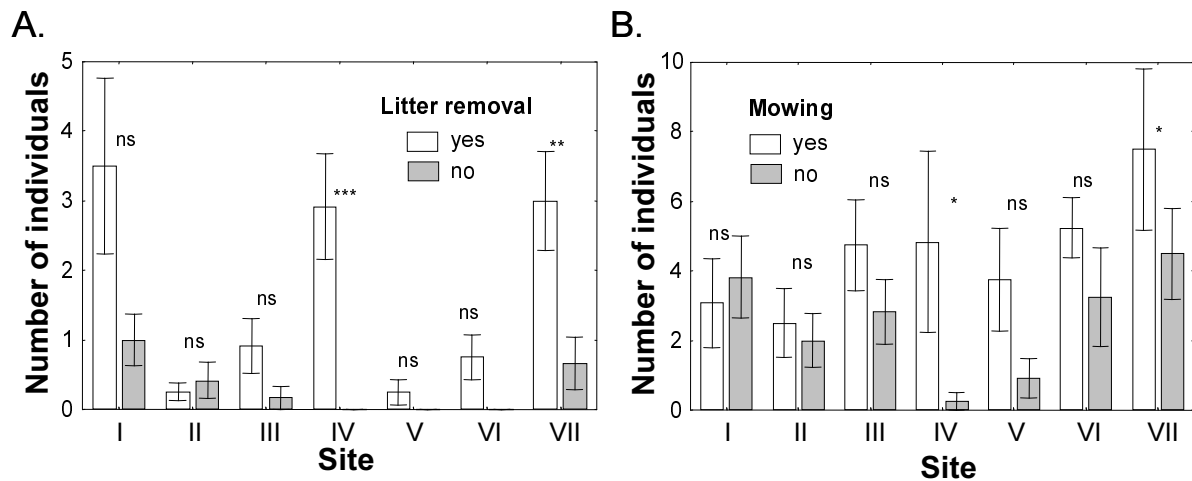


Fig. 4. Number of individuals of *Silene flos-cuculi*, recruited out of sown seeds. **A.** - related to factor “litter” in the first season. **B.** Related to factor “mowing” in the second season. Significances of Mann-Whitney U-test are given as followed: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$. Mean and standard error are shown.

Positive effects of litter removal on the recruitment of *Silene flos-cuculi* seedlings on oligotrophic meadows were also found by Špačová et al. (1998). We assume, the effects of litter or biomass removal were most important at sites with comparatively high aboveground biomass despite of low nutrient availability. Site IV with relatively low soil pH and slow decomposition and site VII dominated by large sedges are both sites producing high amounts of litter, which hampered the recruitment of our study species in plots without litter removal. For transplanted individuals the litter layer plays a minor role, because the initial stage, sensitive to hampering through litter, has been left out. The assumption that the regeneration niche and the main factors affecting establishment and survival can differ between seedlings and adult plants (Shipley et al. 1989, Hitchmough 2003) could be confirmed by the result, that transplant biomass was neither dependent on mowing, nor on litter removal.

Biere (1996) showed that different genotypes of *Silene flos-cuculi* differed in their reaction on soil nutrition. In his study adaptation of specific populations on nutrient availability of their sites was of greater importance than the selective effect of competition. As the seeds

of *Silene flos-cuculi* used in our experiment were collected in a nutrient-rich site, we possibly deal with genotypes, adapted to such conditions. This could be an explanation for the development of larger rosettes on sites V-VII. As no genetic analyses had been carried out in our study, we can not proof this supposition.

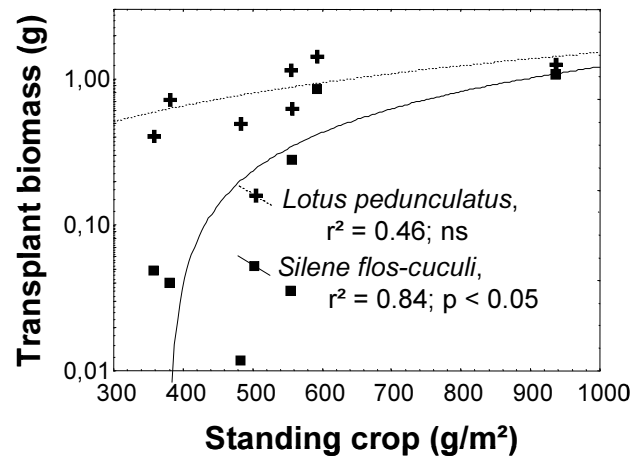


Figure 5. Relation between standing crop and the average biomass of transplants of *Lotus pedunculatus* and *Silene flos-cuculi* on seven fen grassland sites.

The comparatively low survival of transplants in the first season can be explained by the extremely dry summer of 2003. In this case a persistent litter layer could even have had positive effects on individuals by keeping moisture in the soil. At site VI more transplants survived in plots without litter removal and/or mowing than in comparatively open plots with less aboveground biomass. Moisture conditions were considered to be more important for plant survival than the density reduction in the surrounding community through treatments (e.g. Fowler 1988, Eckstein & Donath 2005).

A further explanation for the low numbers of individuals in sown plots in summer 2003 could be, that induced seed dormancy might be increased due to high temperatures (e.g. Baskin & Baskin 1988), so that some sown seeds germinated in 2004.

It is assumed, that under high nitrogen input, Fabaceae lose their competitive advantages in grasslands and their amount in the plant community decline (e. g. Suding et al. 2005). At our study sites *Lotus* seemed to have some advantages in competition for light in comparison to *Silene* due to its shoot morphology rather than due to its nitrogen fixation ability. Under the hydrological conditions, observed at the experimental sites, the efficiency of nitrogen fixation is assumed to be low due to the low oxygen content in groundwater-saturated soil (Kitou & Yoshida, 1990). In our case juvenile plants of *Silene flos-cuculi* appeared to be a weaker competitor than of *Lotus pedunculatus*. At the most eutrophic sites V and VI small rosettes of *Silene* were often overgrown by *Cirsium palustre*, which recruited

out of the soil seed bank after disturbance (pers. observations), while *Lotus* with its elongated shoots was less affected by competition.

The recruitment and establishment of sown species at sites with different nutrient availability and standing crop could be interpreted in the context of the Shifting Limitations Hypothesis (Foster 2001, Foster et al. 2004). We consider nitrogen availability and standing crop to be the main regulating factors in the investigated sites. According to the hypothesis, in the gradient from low productive to high productive sites a shift from dispersal to microsite limitation is assumed. Thus, seed addition should be most successful at sites with low soil nitrogen content and standing crop. This tendency is observed for both species in the experiment. However, it is less distinct than e.g. in the similar designed experiment of Foster (1999). One possible explanation could be, that the sites analysed by Foster differed more than 20 fold between the sites with the lowest and highest standing crop. In our case the difference was only about three fold for standing crop and eight fold for soil nitrogen, although this is nearly the maximum variety, observed for fen grassland communities in Northern Germany (Schrautzer 2004). The results of Reader et al. (1994) also confirm the assumption, that at least three fold differences in standing crop are necessary to observe significant effects of aboveground competition on the biomass of their study species. In our study, the effect of standing crop on seedling establishment was more pronounced, than the effect of soil nutrient availability.

The fact, that both *Silene* and *Lotus* established at the study sites after seed addition, where they were not present before, or their density increased in comparison to the natural population density, shows, that experimental sowing as measure to abolish dispersal limitation was efficient (Tilman 1997, Zobel et al. 2000). The comparatively low differences in standing crop and soil nitrogen content between our study sites made it possible for both studied species to establish at all sites with different productivity.

Plate II



Picture 3. Site V (Upper Eider Valley) of the two-factorial field experiment along a productivity gradient in May 2003.



Picture 4. Seedlings of *Silene flos-cuculi* L. at site IV (Vollstedter See) of the productivity gradient experiment in June 2003. "Bad chances for small seedlings to survive in thick litter layers".

Seed content and conservation evaluation of hay material of fen grasslands

INTRODUCTION

Moderately used semi-natural grasslands have strongly declined in western Europe during the recent decades, because they have been either abandoned or turned into heavily fertilised meadows and pastures (e.g. Ihse 1995, van Dijk 1991, Wheeler 1988). This development led to a loss of species diversity at many grassland sites and probably also at the landscape scale (Losvik 1999, Luoto et al. 2003). Thus, conservation and restoration of species rich grasslands can be considered one of the most important aims of environmental policy in Europe (e.g. Muller et al. 1998, Pykälä 2000).

The primary botanical focus of the conservation of fen grasslands (one of the most species rich European grassland types) is to protect species which are particularly characteristic of this habitat and/or which are regionally rare or endangered. Site conditions and the number and quality of available seeds are two main factors influencing the success of fen grassland restoration (Pfadenhauer & Grootjans 1999).

Topsoil removal is thought to be an appropriate method to restore site conditions in fens since it leads to higher groundwater levels and a reduction of nutrient availability (Van Diggelen et al. 1997, Van Duren et al. 1998). However, target communities generally do not establish after the restoration of site conditions because viable seeds of characteristic species are often absent both in the soil seed bank due to their low longevity and in the seed rain due to dispersal limitation (Bekker et al. 1997, Jansen et al. 1996, Jensen 1998, McDonald et al. 1996).

Hay transfer is one possible method to restore species diversity of vascular plants in degenerated, but formerly species-rich semi-natural grasslands. Experiments on the restoration of calcareous (Miller & Pfadenhauer 1997), fen (Biewer & Poschlod 1997, Patzelt et al. 2001), and floodplain grasslands (Hölzel & Otte 2003) showed successful establishment of many characteristic species as a result of hay transfer. Hay from species-rich donor sites is harvested when the seeds of most of the species have ripened, moved

over and spread out in a thin layer at the recipient site. The method has advantages as it is cheap, easy to carry out and that well adapted autochthonous ecotypes are used, which may have higher establishment rates than those of commercial seed mixtures (Jones & Hayes 1999, Pfadenhauer & Grootjans 1999). Thus, hay transfer for restoration purposes have become more and more popular during recent years.

Of course, the selection of a source community for hay transfer is of paramount importance for the success of restoration measures. Most authors, e.g. Hölzel & Otte (2003) have chosen their donor sites for hay transfer by observing solely the species composition of vegetation. In this study we present a new method to select donor sites for hay transfer based additionally on the presence, number and viability of seeds in hay. This method can improve the success of restoration measures, especially if several suitable donor sites are available.

So far, only few studies have analysed the number and viability of seeds in hay material directly (Smith et al. 1996, Wells et al. 1986) or performed germination experiments to investigate the seed content in the samples of hay material, used for transfer (Biewer & Poschlod 1997).

This study aims to analyse the seed content of hay from five different communities and to check the viability of seeds in order to evaluate the most suitable donor site for a planned hay transfer on degenerated fen grasslands in the upper Eider valley in Northern Germany (Jensen et al. 2001).

The main questions were:

- How many species of the aboveground vegetation are represented in the hay as seeds?
- How large is the seed content of the hay of different communities?
- Are seeds of rare or endangered species (target species) present in the hay?

METHODS

Study sites

We examined two species-rich fen grassland sites in Northern Germany (Tröndelsee [TS], 54°18'24''N/10°10'20''E; Lehmkuhlener Stauung [LS]; 54°12'24''N/ 10°20'27''E). The grasslands are regularly mown once a year (TS in the middle of July, LS at the end of August). We chose two plots in LS and three plots in TS (each 25 m², Tab. 1) in order to analyse the species composition of the above ground vegetation and the seed content of the hay of these communities.

Table 1. Description of study plots.

Study Site	Plant community
LS I	sedge-dominated fen meadow with low phytomass [Campylio-Caricetum dioicae]
LS II	sedge-dominated fen meadow with high phytomass [Caricetum rostratae]
TS I	herb-dominated fen meadow [Angelico-Cirsietum oleracii]
TS II	Carex disticha Huds. - dominated fen meadow
TS III	Carex flava agg. - dominated fen meadow

Sampling

On each of these 25 m² plots a vegetation relevé was carried out according to the method of Braun-Blanquet (1964), modified after Dierssen (1990) and following the nomenclature of Wisskirchen & Haeupler (1998).

Five 0.25 m² subplots (replicates) were randomly chosen within each plot and the phenologic conditions (vegetative, flowering, fruiting) of the occurring species were noted. Standing crop of the subplots was manually harvested and transferred to the laboratory as separate samples. Harvesting took place one week before the mowing date of the study sites (11.07.2000 at TS, 20.08.2000 at LS). The harvested material was dried at 28 °C and weighed.

Seed content

The plant material harvested in the subplots was manually separated into the following three fractions: (i) seeds detected by eye [sf], (ii) rough plant material without seeds [rpm], and (iii) fine plant material expected to contain seeds [fpm]. The sf-and fpm-fraction were used for further examinations. The word “seed” is used in a rather wide sense in this study including both seeds and one-seeded fruits (e.g. caryopses of Poaceae, achenes of Asteraceae).

After moist stratification at 3 °C for five weeks the fpm-samples were spread in a thin layer on sterilised garden soil (TKS-II) and placed in a climate chamber (25/15 °C, day/night rhythm). In the following six months (November 2000 – April 2001) the samples were watered regularly and all occurring seedlings were identified, counted and removed.

The seeds of the sf-fraction were identified and counted under a binocular magnifier. In some cases (*Juncus* spp., Orchidaceae) the number of fruits instead of the number of seeds was recorded. The number of seeds of each species and sample resulted from the total

number of seeds from the sf-fraction and the number of seedlings from the fpm-fraction. Using this data, we calculated the seed content per square metre for each plot.

Germination and viability test

For each species, which was represented by at least five seeds in the sf-samples, a germination test was carried out. Germination was tested separately if species were found in TS as well as in LS samples. After moist stratification at 3 °C for five weeks seeds were put on filter paper in Petri dishes and placed in a climate chamber (25/15 °C, day/night rhythms) and were watered regularly. All germinated seeds were counted during a 10-week period. Additionally, the seeds, which had not germinated, were tested by pinching them with a needle in order to see if they contained firm embryo and, at least potentially, could be viable (Baskin & Baskin 1998). For *Juncus* spp. whole fruits were used for the germination test and the number of germinated seeds per fruit was calculated; in this case the viability test could not be performed.

Evaluation of possible donor sites

The primary botanical focus of fen grassland conservation is to protect (i) species which are particularly characteristic of this habitat (ii) and species which are regionally rare or endangered.

From this point of view, we calculated a rarity weighted fen grassland species score (RWFSS, Wheeler 1988) in order to evaluate which of the analysed communities would be the best for the planned hay transfer. This index is based on the number of characteristic fen grassland species and the number of rare or endangered species represented in the hay material of each plot.

All species of fens (Scheuchzerio-Caricetea) and of wet meadows (Molinietalia) were designated as characteristic fen grassland species (cfs) and the number of these species was counted for each plot (\sum_{cfs_i} ; see Dierssen et al. 1988, Wheeler 1988). Furthermore, the sum of the score points of regionally rare or endangered species (rfs) was calculated (\sum_{rfs}). For this purpose, the occurrence of species listed in the regional Red Data Book (Mierwald & Beller 1990) was weighted: Species of category 1 (strongly endangered) got three score points, species of category 2 (endangered) got two score points and species of category 3 (rare) got one score point. We calculated the rarity weighted fen grassland species score as

$$RWFSS = \sum (cfs + rfs).$$

Data analysis

The relation between the seed content of the hay and the species composition of the aboveground vegetation of the studied communities was determined by using the Ward-index for a cluster analysis by the complete-linkage method. Prior to analysis a z-transformation of data was carried out.

In the germination experiment we calculated the germinability of seeds of three species groups (herbs, sedges and grasses) as a mean germinability of studied species from each group for each site and used ANOVAS to test the differences in germinability and viability between these groups. To fulfil the ANOVA conditions, the data (percentage viability and germinability) were arcsin-transformed. Tukeys-honest-significant-tests (HSD) were used for post hoc comparisons (Sokal & Rohlf 1995).

Differences in the RWFSS were also tested by ANOVA. The ANOVA assumptions were fulfilled after square root transformation of the data. All statistical analyses were carried out with the PC-program Statistica (Statsoft 1998).

RESULTS

Species composition and number of established vegetation

Species number in the aboveground vegetation varied between 29 species in TS II and 41 species per 25 m² in LS I. All studied areas were dominated by small sedges, at TS I *Filipendula ulmaria* (L.) Maxim. reached high abundance, at TS II herbs (*Angelica sylvestris* L., *Cirsium oleraceum* (L.) Scop.), at TS III reed (*Phragmites australis* (Cav.) Trin. ex Steud.) and at LS II low productive grasses (*Agrostis canina* agg., *Festuca rubra* agg.). The RWFSS-index of the entire 25 m² plots was 14 for TS II, 17 for TS I, 25 for LS II, 26 for TS III and 39 for LS I (Tab. 2).

Seed content in the hay

The number of seeds per square-metre ranged significantly from about 2 000 in LS I to 12 000 in TS III (one-way ANOVA, $F = 4.65$, $p < 0.01$), the mean seed content for all plots was approximately 7 000 seeds per m². Standing crop varied significantly between 350 g/m² in LS I and 750 g/m² in LS II (one-way ANOVA, $F = 9.36$, $p < 0.001$; Fig.1).

In LS I, *Rhinanthus angustifolius* agg., *Juncus articulatus* L. and *Briza media* L. were the most frequently represented seeds in the hay. In LS II seeds of *Agrostis canina*, *Carex nigra* (L.) Reichard and *Carex panicea* L. were found most often. The hay material of TS I

Table 2. Species composition of the aboveground vegetation (AV) and mean number of seeds per square-metre in the hay material of the five studied plots. LS: Lehmkuhlener Stauung, TS: Tröndelsee. First number - seeds found by manual sorting, second number - seedlings germinated from fpm-fraction.

Red data book	Species name	LS I		LS II		TS I		TS II		TS III	
		AV	Number of seeds per square metre	AV	Number of seeds per square metre	AV	Number of seeds per square metre	AV	Number of seeds per square metre	AV	Number of seeds per square metre
3	<i>Carex panicea</i> L.	2a	139/0	2m	920/0	2b	674/0			2m	361/0
	<i>Agrostis canina</i> L.	2m	0/12	3	2460/1103		0/5		0/7	2m	0/2
	<i>Anthoxanthum odoratum</i> L.	2m	26/3	2m	199/10	2m	2/2		0/1		
2	<i>Briza media</i> L.	2m	240/6								
1	<i>Carex dioica</i> L.	2m	101/0								
3	<i>Carex echinata</i> Murray	2m	5/0	2m	34/1		1/0			2m	738/14
	<i>Carex nigra</i> (L.) Reichard	2m	4	2m	2362/0	2m	146/0				
	<i>Cerastium holosteoides</i> Fr.	2m	0/11	2m	0/1	2m	124/114	2m	192/69	+	0/3
	<i>Cirsium palustre</i> (L.) Scop.	2m	1/0	+	0/1	2m	0/1	2m	472/8		
	<i>Epilobium ciliatum</i> Raf.	2m	194/10		0/1	2m	0/1	2m	0/1	1	
	<i>Festuca rubra</i> L.	2m	34/60	2b	254/211	2m	107/30	2m	290/112	2m	
	<i>Galium palustre</i> L.	2m	1/0	2m	479/104	2a	882/190	2m	60/14	2m	0/2
	<i>Holcus lanatus</i> L.	2m	55/5	2a	22/0			2m	28/0	2m	1766/0
	<i>Juncus articulatus</i> L.	2m	356/2								
	<i>Luzula multiflora</i> (Ehrh.) Lej.	2m	22/0	2m	30/0						
2	<i>Pedicularis palustris</i> L.	2m	99/0								
	<i>Prunella vulgaris</i> L.	2m	49/1		0/1						
	<i>Ranunculus acris</i> L.	2m	214/2	+	0/3	1	83/0	2m		2m	80/0
3	<i>Rhinanthus argusifolius</i> agg.	2m	350/0			2a	535/0	2m	246/0	1	73/0
	<i>Scutellaria galericulata</i> L.	2m	9/0	2m	10/0						
	<i>Trifolium repens</i> L.	2m	9/0								
	<i>Silene flos-cuculi</i> (L.) Clairv.	1	29/2				0/1			+	398/14
	<i>Caitha palustris</i> L.	1	5/0								
	<i>Rumex acetosa</i> L.	+	2/0	+	4/0	2m	9/1	+	0/1	1	
	<i>Equisetum fluviatile</i> L.	2a		2m		1					
3	<i>Viola palustris</i> L.	2a		2m							
3	<i>Menyanthes trifoliata</i> L.	2a		+							
	<i>Filipendula ulmaria</i> (L.) Maxim.	2a		2m		2b		2b		2b	
	<i>Potentilla erecta</i> (L.) Raeusch.	2a		2m						2m	
	<i>Potentilla erecta</i> (L.) Raeusch.	2m		2m		2m				2m	
	<i>Lotus pedunculatus</i> Cav.	2m		2m		2m				2m	
	<i>Potentilla palustris</i> (L.) Scop.	2m		2m		2m				2m	
3	<i>Carex demissa</i> Hornem.	2m		+		2m		2m		2m	3000/0
3	<i>Galium uliginosum</i> L.	2m									
3	<i>Danthonia decumbens</i> (L.) DC.	2m									
	<i>Plantago lanceolata</i> L.	2m									
3	<i>Dactylorhiza majalis</i> (Rchb.) Hunt & Summerhayes	1				2a	312/57	2m	0/2	+	
	<i>Salix spec.</i>	1									
	<i>Mentha aquatica</i> L.	+		2m				1			
	<i>Lythrum salicaria</i> L.	+		+		r					
2	<i>Parnassia palustris</i> L.	+									
	<i>Quercus robur</i> L.	+									
	<i>Rumex acetosella</i> L.	r	0/2				0/2				0/1

Table 2. (continued)

Red	Species name	LS I		LS II		TS I		TS II		TS III	
		AV	Number of	AV	Number of	AV	Number of	AV	Number of	AV	Number of
3	<i>Valeriana dioica</i> L.		2/0							1	
	<i>Lysimachia vulgaris</i> L.		1/0	2a				+		2a	
	<i>Betula spec.</i>		1/0								
3	<i>Juncus effusus</i> L.			2m	1/0	1	1/0	2m	1/1	2m	244/0
	<i>Angelica sylvestris</i> L.			2m	210/2	1		2m	187/3		
	<i>Carex rostrata</i> Stokes			2m	339/0	1		2b			
	<i>Eriophorum angustifolium</i> Honck.			2m	640/0						
	<i>Ranunculus flammula</i> L.			2m	3/0						
	<i>Carex disticha</i> Huds.			2m	28/1			2a	57/1	3	2/0
	<i>Carex acutiformis</i> Ehrh.			2m		2a	8/0			2m	
	<i>Persicaria lapathifolia</i> (L.) Delarbre			2m		2m	27/32	2m	7/27	2m	48/29
	<i>Poa trivialis</i> L.				0/1	2m					
	<i>Sonchus oleraceus</i> L.				0/2						
	<i>Deschampsia cespitosa</i> (L.) P. Beauv.					1	368/0	2m	1440/0	1	
	<i>Geum rivale</i> L.					2m	2/0			2m	
	<i>Scirpus sylvaticus</i> L.					2a		1			
<i>Hypericum tetrapterum</i> Fr.					2a		2m				
<i>Ajuga reptans</i> L.					2m						
<i>Veronica chamaedrys</i> L.					2m						
<i>Vicia cracca</i> L.					1		1		2m		
<i>Lathyrus pratensis</i> L.					+		r		1		
<i>Calystegia sepium</i> (L.) R. Br.					1						
<i>Stellaria palustris</i> Ehrh. ex Hoffm.					1				2m	13/0	
<i>Phragmites australis</i> (Cav.) Trin. ex Steud.					+				2b		
<i>Salix cinerea</i> L.					+						
<i>Achillea millefolium</i> agg.					r						
<i>Cynosurus cristatus</i> L.								+	47/0		
<i>Cirsium oleraceum</i> (L.) Scop.								2b			
<i>Agrostis stolonifera</i> agg.								2m			
<i>Carex hirta</i> L.								2m			
<i>Equisetum palustre</i> L.								2m			
<i>Epilobium angustifolium</i> L.								+			
<i>Persicaria amphibia</i> (L.) Delarbre											
<i>Carex lepidocarpa</i> Tausch										3000/0	
<i>Cardamine pratensis</i> L.										0/1	
<i>Myosotis scorpioides</i> agg.										1/0	
<i>Alnus glutinosa</i> (L.) P. Gaertn.										15/0	
<i>Galeopsis tetrahit</i> L.										1/0	
<i>Ranunculus repens</i> L.											
<i>Anemone nemorosa</i> L.											
<i>Calamagrostis canescens</i> agg.											
<i>Cardamine amara</i> L.											
<i>Festuca pratensis</i> Huds.											
<i>Carex ovalis</i> Good.										+	
RWFSS of vegetation											26
											14
											17
											25
											39

Red data book: 1: strongly endangered, 2: endangered, 3: rare (Mienwald & Beller 1990). Aboveground vegetation cover after Braun-Blanquet (1964), Dierssen (1990).

was dominated by *Carex panicea* L., *Holcus lanatus* L. *Rhinanthus angustifolius* agg., that of TS II by *Cirsium palustre* (L.) Scop. *Deschampsia cespitosa* (L.) P. Beauv. and *Festuca rubra*. The high seed content in the hay material of TS III resulted from a large number of seeds of some particular sedges (*Carex echinata* Murray, *C. lepidocarpa* Tausch, *C. demissa* Hornem.), *Juncus articulatus* L. and herbs (*Silene flos-cuculi* (L.) Clairv.) whereas seeds of grasses were hardly found on this plot (Tab. 2).

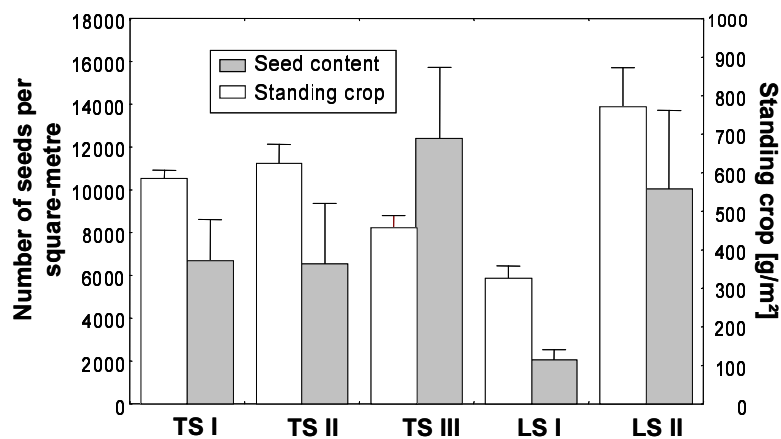


Figure 1. Mean seed content and dry weight of hay material of the five investigated plots (TS I - TS III: Tröndelsee; LS I, LS II: Lehmkuhlener Stauung). Error bars indicate standard error.

Relationship between the established vegetation and hay

41–47% of the species occurring in the aboveground vegetation were represented as seeds in the hay material of the TS-plots. In the LS-plots the percentage of species of the aboveground vegetation that were also found in the hay was 71% (Tab. 3).

Table 3. Species number (sum of five subplots of 0.25 m²) in the aboveground vegetation and the hay-material of the five investigated plots.

Plot		LS I	LS II	TS I	TS II	TS III
1	Aboveground vegetation (AV)	41	31	34	29	37
2	Hay-material (HM)	35	28	22	18	21
2a	Present in AV	29	21	16	12	16
2b	Absent in AV	6	7	6	6	5
	Relation between (2a) and (1) [%]	71	71	47	41	41

No correlation between the abundance of species in aboveground vegetation and the amount of seeds in the hay (Spearman rank correlation) was found for any study site (TS I, $r = -0.183$; TS II, $r = 0.025$; TS III, $r = 0.062$; LS I, $r = 0.048$; LS II, $r = 0.065$); all $p > 0.05$.

Ranunculus acris L. and *Pedicularis palustris* L. showed only low germination percentages although most of the seeds were viable (Tab. 4).

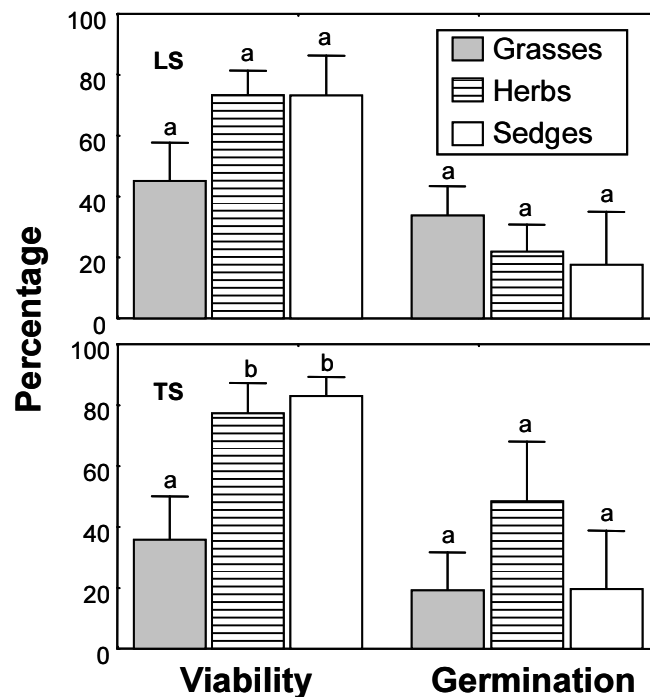


Figure 3. Mean percentage viability and germination of grasses, herbs and sedges of the hand-sorted seeds (sf-fraction) from the hay material of Lehmkuhlener Stauung (LS) and Tröndelsee (TS). Error bars indicates standard error.

We found no significant differences in mean germination percentage between the species groups, neither at TS nor at LS ($F = 0.9$, $p = 0.4$; $F = 0.5$, $p = 0.6$; Fig. 3). For some species germination percentage and viability of seeds differed between TS and LS. While 74% of the seeds of *Cirsium palustre* L. were viable in TS only 41% in LS contained firm endosperm.

Similar differences were found e.g. for *Rhinanthus angustifolius* and *Ranunculus acris*.

Conservation evaluation

The RWFSS was highest in LS I and in TS III and was significantly lower on the other communities ($F = 18.1$, $p < 0.001$). Ten rare and endangered species were found in the hay samples of all five investigated plots, most of them were found in the LS I samples (eight species) and the TS III samples (five species; Fig. 4).

Table 4. Number of seeds of the species, used for germination test and their germinability/ viability on the sites (LS: Lehmkuhlener Stauung, TS: Tröndelsee).

Tested species	N		Germinated		% germinated		Viable		% viable	
	LS	TS	LS	TS	LS	TS	LS	TS	LS	TS
<i>Agrostis canina</i>	150		111		74		111		74	
<i>Angelica sylvestris</i>	300		0		0		47		15.7	
<i>Anthoxanthum odoratum</i>	80		47		58.8		49		61.3	
<i>Briza media</i>	100		16		16		23		23	
<i>Carex acutiformis</i>		12		0		0		10		83.3
<i>Carex dioica</i>	188		2		1.1		182		96.8	
<i>Carex disticha</i>		41		0		0		31		75.6
<i>Carex echinata</i>	102	215	89	208	87.3	96.7	96	215	94.1	100
<i>Carex flava</i>		300		1		0.3		194		64.7
<i>Carex nigra</i>	300		0		0		197		65.7	
<i>Carex panicea</i>	116	255	0	0	0	0	97	234	83.6	91.8
<i>Carex rostrata</i>	300		0		0		79		26.3	
<i>Cerastium holosteoides</i>		155		155		100		155		100
<i>Cirsium palustre</i>	70	340	4	54	5.7	15.9	29	252	41.4	74.1
<i>Dantonia decumbens</i>	65		21		32.3		64		98.5	
<i>Deschampsia cespitosa</i>	68	300	1	23	1.5	7.7	4	26	5.9	8.7
<i>Epilobium spec.</i>	100		85		85		89		89	
<i>Festuca rubra</i>	96	36	23	20	24	55.6	24	20	25	55.6
<i>Filipendula ulmaria</i>	300		5		1.7		104		34.7	
<i>Holcus lanatus</i>	192	300	4	41	2.1	13.7	4	41	2.1	13.7
<i>Lysimachia vulgaris</i>	285		2		0.7		285		100	
<i>Mentha aquatica</i>	45		0		0		45		100	
<i>Pedicularis palustris</i>	100		3		3		52		52	
<i>Plantago lanceolata</i>		250		197		78.8		244		97.6
<i>Poa trivialis</i>	92	17	55	0	59.8	0	65	11	70.7	64.7
<i>Prunella vulgaris</i>	37		31		83.8		33		89.2	
<i>Ranunculus acris</i>	115	69	14	0	12.2	0	115	29	100	42
<i>Ranunculus flammula</i>	35		8		22.9		35		100	
<i>Rhinanthus angustifolius</i>	94	303	0	0	0	0	92	163	97.9	53.8
<i>Rumex acetosa</i>	5		3		60		3		60	
<i>Scutellaria galericulata</i>	24		2		8.3		17		70.8	
<i>Silene flos-cuculi</i>		300		286		95.3		286		95.3

DISCUSSION

Species with large seeds like *Carex* ssp., *Rhinanthus angustifolius* or *Dantonia decumbens* (L.) DC were detected to almost 100% by manual sorting whereas seeds of many species with smaller seeds (e.g. *Agrostis canina*, *Cerastium holosteoides*) were rarely found by this method. However, seedlings of these small-seeded species built up the main component of all seedlings germinating from the fpm-fraction (Table 3). Due to the combination of the two methods it is likely that most of the species present in the hay were detected.

Vegetation relevés deliver information about presence and abundance of target species on the studied sites and could be used for determination of their relevance as donor habitats (Strykstra 2000), but the question about the quality of hay material remains open, if only the vegetation is analysed.

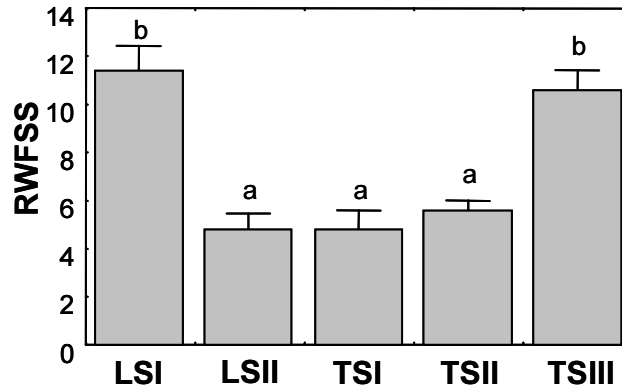


Figure 4. Mean rarity weighted fen grassland species score (RWFSS) of the hay material of the five investigated plots (TS I—TS III: Trøndelsee; LS I, LS II: Lehmkuhlener Stauung). The index is based on number of characteristic fen grassland species and the number of regionally endangered species (see: Methods). Error bars indicate standard error.

We found that between 41% and 71% of the species present in the aboveground vegetation were represented as seeds in the hay material. Species differ with respect to their flowering and fruiting phenology and thus it seems to be unlikely that all species of the aboveground vegetation are present in hay material which was cut at one specific date (Patzelt et al. 1997, Pfadenhauer & Grootjans 1999). The date for this investigation was chosen according to the regular mowing date of the sites for conservation purposes (TS: middle of July; LS: beginning of August). The viability of some species, especially grasses, could be affected by the mowing time, as these were not completely ripe. Some target species like *Parnassia palustris* L. (seed ripening in September) or *Viola palustris* L. (seed ripening in May/June) present in vegetation on the site LS could not be detected as seeds in the hay because their seed ripening period differs from the mowing date. Seeds of these species were absent in the samples. However, a few seeds of species that had released their seeds before mowing (e.g. *Cardamine pratensis* L., *Rumex acetosa* L. or *Valeriana dioica* L.) were also detected in the hay in small number (see also Patzelt et al. 1997). We assume that these seeds were picked up with litter material when raking the hay from the soil surface. Furthermore, some seeds of anemochorous species (e.g. *Alnus glutinosa* (L.) P. Gaertn., *Rumex acetosella* L. or *Sonchus oleraceus* L.) appeared in the hay samples although they were absent in the aboveground vegetation. These mainly ruderal species

might be of importance for vegetation succession at the restoration sites after a hay transfer even if they occur only in low quantities.

Although we did not find similar studies that compare species composition of seeds in hay material with those of the aboveground vegetation, investigations of species establishment after hay transfer show that it is impossible to establish the whole species composition of a donor site by only one hay transfer. Biewer & Poschlod (1997) found that approximately 80% of the species of the donor site were able to establish in a restored fen meadow after hay transfer and Patzelt & Pfadenhauer (1998) mentioned that 50–70% of the species of the donor site established at the acceptor site after hay transfer (see also Patzelt et al. 2001). Similar results were obtained by Miller & Pfadenhauer (1997) in calcareous grasslands, by Kirmer & Mahn (1996) in restoration experiments in brown coal mines and by Hölzel & Otte (2003) in floodplain meadows. Analysing the seed content of available hay prior to hay transfer allows more accurate predictions about the expected species composition on restored sites.

Biewer & Poschlod (1997) estimated seed content in litter meadows (*Molinietalia*) to be 4 000–7 000 seeds per m² based on observations on the seed production of all species in the vegetation. This is in good accordance with the results of the present study in which a mean seed content of 7 000 seeds per m² was found, but much lower, than the estimated annual seed rain of abandoned fen grasslands (18 000 – 87 000 seeds per m², Jensen 1998).

The low germination percentage especially of the herbs and the sedges as compared to the viability of the seeds is probably caused by seed dormancy. Although all fpm-samples were stratified at 3 °C for five weeks this obviously did not break dormancy in all cases. The sedges especially showed high viability, but they usually did not germinate under the tested conditions. Sedges often are characterised by a pronounced primary dormancy (Schütz 1998, Schütz & Rave 1999) and some species need long stratification periods for dormancy release (e.g. *Carex panicea*; Jensen 2004). Furthermore, pronounced seasonal changes in dormancy are known from the genus *Rhinanthus* ssp. in which germination exclusively occurs in late winter (Jensen 2004, Pons 1991). This explains our result that the viability of seeds of *Rhinanthus* was nearly 98% in TS whereas no seedlings occurred in the germination test (which was carried out in spring 2001).

The hay material of LS I and TS III was characterised by the highest RWFSS-value. Taking into account that LS I had a high similarity between aboveground vegetation and species composition of the seeds in the hay material we decided to choose LS I as donor community for the hay transfer experiment in the Upper Eider Valley. Furthermore LS I is characterised by the highest species diversity in the hay. The low seed content per square metre (see Fig. 1) does not appear to be a problem for restoration measures as it is mainly

caused by the relatively low standing crop of the site. The mean seed content per kilogram of hay in LS I (6 000 seeds) was about half that of most other sites (11 000–12 000 in TS I, TS II and LS II). The low productivity of LS I can be seen as prerequisite of its high species diversity as we found a negative relation between standing crop and diversity in the aboveground vegetation of all investigated plots ($r = - 0.41$, $p < 0.05$; see also Wheeler & Shaw 1991).

CONCLUSIONS AND IMPLICATIONS FOR NATURE CONSERVATION

According to Lawson et al. (2004) the successful creation of species-rich grassland strongly depends on seed addition to overcome seed-limitation and on site conditions and management of the restoration site (see also Strykstra 2000). As mentioned in the introduction, hay transfer (as one measure of seed addition) has been increasingly applied during the last two decades. Based on the results of the present study, we recommend that not only the restoration site should be carefully chosen, but that also the best fitting donor site for gaining species rich hay material should be selected for achieving restoration success.

Furthermore we conclude that it is possible to analyse and evaluate the seed content of the hay of different species-rich grassland sites in a comparatively short period of time (during winter). Thus, we recommend the method presented in this study, when choosing the optimal donor site for a future hay transfer is in question in grassland restoration. This method is likely to be more precise than a sole analysis of the established vegetation as seed production and germinability usually do not correlate with species abundance or biomass.

Plate III



Picture 5. Hay from the Lehmkuhlener Stauung (LS I) freshly harvested for the investigation of seed content in August 2000.



Picture 6 and 7. Flowering individuals of *Rhinanthus angustifolius* C.C. Gmel (left) and *Pedicularis palustris* L. at the selected site for hay transfer (Lehmkuhlener Stauung: LS I) in July 2000.

Effects of topsoil removal, seed transfer with plant material and moderate grazing on restoration of riparian fen grasslands

INTRODUCTION

Losses of species diversity in fen grasslands were observed in the recent decades all over Europe (e.g. Joyce & Wade 1998, Prach et al. 1996). The main reason of these processes can be seen in the changes of traditional agricultural usage of wet habitats in favour of intensive farming with an extensive use of fertilizer on the one and abandonment of less productive sites on the other hand during the last 50 years (e.g. Vos & Opdam 1993).

Restoration of degraded fen grasslands includes the reestablishment of traditional land use (low intensity management, e.g. large scale moderate grazing or mowing, Bakker 1989). Nevertheless the reestablishment of traditional land use alone is often insufficient for restoration of species diversity and re-colonisation of the sites by target species, after they became locally extinct (Jansen et al. 1996, Poschlod et al. 1998). High soil fertility of degraded sites remains a key factor limiting species diversity (e.g. Cornwell & Grubb 2003). The reduction of nutrients at restoration sites by means of traditional land use remains often below the expectation (Gusewell et al. 2000) or takes a longer period of time, as practicable (e.g. Hellström et al. 2003). Especially on soils with high content of organic matter (e.g. peat soils) the reduction of nutrients is often difficult due to high N- and P- reserves in the peat.

One way to reduce soil fertility can be the removal of upper mineralized soil layers. In general, topsoil removal has been discussed as one possible restoration measure in recent years (Van Diggelen et al. 1997, Jansen & Roelofs 1996, Manchester et al. 1999) and its practicability was tested in different ecosystems (woods: De Vries et al. 1995; heathlands: van den Berg et al. 2003; different types of grassland: Berendse et al. 1992; fen grasslands: Patzelt et al. 2001, Tallowin & Smith 2001; floodplain meadows: Hölzel & Otte 2003, Vécrin & Muller 2003). Besides the reduction of soil fertility, topsoil removal lead to elimination of dominant vegetation, which is in most cases formed by tall growing forbs, agricultural grasses or ruderals. Target species of nutrient poor ecosystems may profit from the removal

of competitors (e. g. Kotorová & Lepš 1999) and use the patches of bare soil as safe sites for germination and establishment (Bullock et al. 1994, Kotanen 1997).

The second main obstacle on the way to successful restoration of species diversity is often the absence of viable seeds (e.g. Olff & Bakker 1991, Verhagen et al. 2001, Poschlod & Biewer 2005). The cognition, that most species in the landscape are dispersal limited was approved by numerous studies (e.g. Eriksson & Ehrlén 1992, Zobel et al. 2000, Coulson et al. 2001). While the resident plant species dominate the seed rain and soil seed bank (Jensen 1998), target species are underrepresented or they completely disappeared from the soil seed bank and the nearby surrounding of degraded fen grasslands. Rare and endangered species are also supposed to have lower long-distance dispersal ability than common species (Ozinga et al. 2005). Long-distance dispersal processes are rare stochastic events, additionally hampered by landscape fragmentation (e.g. Poschlod et al. 1996, Soons et al. 2005).

To overcome dispersal limitation of target species transfer of hay material from species-rich meadows was proposed. Experiments on the restoration of calcareous (Miller & Pfadenhauer 1997), fen (Biewer & Poschlod 1997, Patzelt et al. 2001), and floodplain grasslands (Hölzel & Otte 2003) showed successful establishment of many target species after hay transfer. Advantages of this method are, that it is easy to carry out, comparatively cheap and that well adapted autochthonous ecotypes are used, which are expected to have higher establishment rates than those of commercial seed mixtures (Jones & Hayes 1999, Pfadenhauer & Grootjans 1999).

To test the effects of traditional management (moderate grazing), topsoil removal and hay transfer (as well as their interactions) on the restoration of species diversity at a fen grassland site, we carried out a three-factorial field experiment in the Upper Eider Valley, a small river valley in N-Germany. Our intent was to study the (i) nutrient reduction, (ii) changes in species composition and dominance as well as the (iii) establishment of target species during four years.

METHODS

Study area

The experimental area is situated within the valley of the Upper Eider River in Northern Germany (54°13' N, 10°01' E). The area is a part of the "Eider Valley pasture landscape", a nature conservation project including the rewetting of fens and establishment of a large-scale moderate grazing system both at fens and adjacent mineral slopes since 1999 (Jensen et al. 2001). The maximum stocking rate is 1.5 cattle/ha. Current vegetation can be described as

vegetation of nutrient rich (abandoned) fen meadows with high abundance of highly competitive forbs, grasses and sedges (e.g. *Urtica dioica*, *Phalaris arundinacea*, *Carex acutiformis*). The peat layer is about 2-3 m thick and the topsoil of about 30-40 cm is strongly mineralised due to drainage (Trepel & Kluge 2002).

Three-factorial experiment

In autumn 2001 a field experiment was established in the moderately grazed fen area in the Upper Eider Valley. Four 12 x 24 m blocks were laid out as split-split-plot design combining three treatments: moderate grazing (yes/no), topsoil removal (yes/no) and hay transfer (yes/no; Fig. 1).

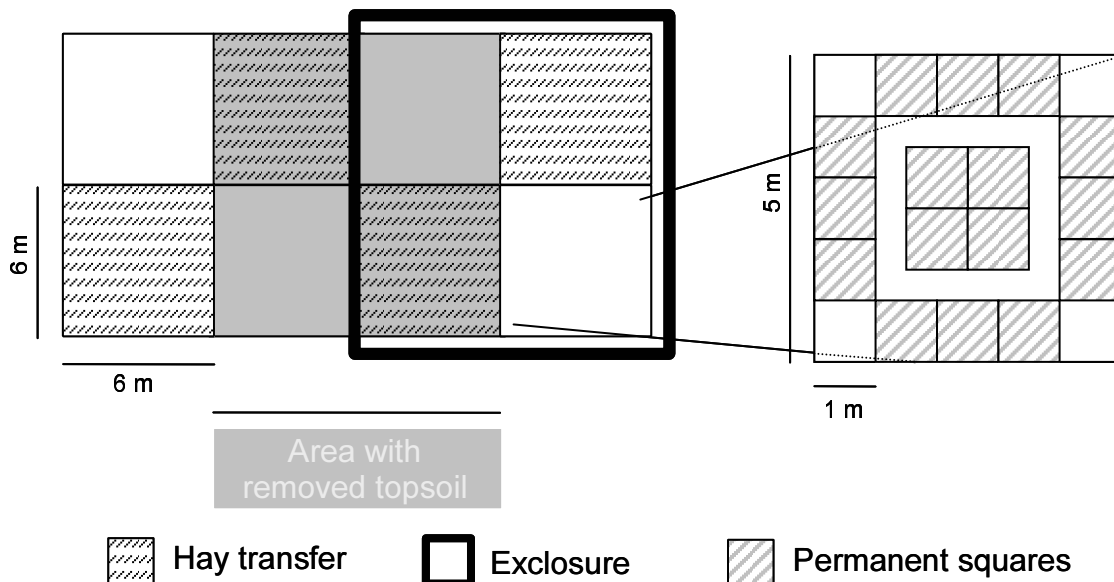


Figure 1. Design of the three-factorial experiment including, the factors grazing (yes, no [enclosure]), topsoil removal and hay transfer. One block of four and the arrangement of permanent squares for vegetation survey within one treatment subplot are shown exemplary.

One half of each block (12 x 12 m) was excluded from grazing by a wire fence, while the other half could be reached by grazing cattle. At plots with topsoil removal (6 x 12 m within each grazing treatment) topsoil was removed by a bucket excavator down to the depth of approx. 30 cm. At hay transfer subplots (5 x 5 m) seed-rich hay material was spread in a 1-3 cm thick layer. At plots without topsoil removal, standing crop was mown and removed from the experimental blocks once before hay transfer (Fig. 1). The seed-rich hay material was harvested after regular mowing end of August 2001 at a species-rich fen meadow (Lehmkuhlener Stauung; 54°12'24"N / 10°20'27"E) and transferred directly to the

experimental site. Seed content and species composition of hay were analysed before the experiment was started (Rasran et al. 2006). In all subplots within each combination of experimental factors 16 permanent squares á 1 m² were chosen for vegetation analyses (Fig. 1). We recorded vegetation cover and dominance of each species using the dominance-based scale of Londo (1975) during four vegetation periods (2002-2005). The sum of cover values of the 16 permanent squares was considered as Cumulative Cover (CC) of each species. The number of permanent squares, in which the species was present, was considered as Cumulative Frequency (CF) of the species.

For further analysis we assigned the species, occurring in the experiment, to one of the following ecological groups:

- SC: Species of nutrient poor fens and bogs (*Scheuchzerio-Caricetea* community)
- MO: Species of moderately used wet hay meadows (*Molinietalia* community)
- EF: Species of nutrient enriched agricultural grasslands (Arrhenatheretea and Lolio-Potentillion communities)
- PH: Tall-growing reed species (*Phragmitetea* community)
- M: Annual and perennial ruderal species, nutrient-rich mud bank community species and miscellaneous, e.g. *Salix* spp.

All members of the first two groups (SC: e.g. *Pedicularis palustris*, MO: e.g. *Silene flos-cuculi*) are considered as target species. Species out of the third group (e.g. *Poa trivialis*, *Ranunculus repens*) has dominated the current vegetation before the experiment was started.

The nomenclature followed Wisskirchen & Haeupler (1998).

Groundwater and soil properties

Groundwater levels were measured monthly for each experimental block separately at areas with and without topsoil removal.

As the soil surface of areas with topsoil removal laid 30 cm deeper than the surrounding, drainage was necessary to avoid long-term inundation at some sites.

Nitrogen, phosphorus, potassium and magnesium were measured from soil samples from 0-15 and 15-30 cm depth separately at areas with and without topsoil removal at each block at the beginning of the experiment (2001) and again after four years (2005). For that

purpose we took mixed soil samples of five cores taken randomly within the treatment plots using a 3.5 cm diameter corer. In 2005, additional six mixed soil samples were taken at the donor site for hay material as an example for the nutrient status of a “target community”.

Nutrient analyses were performed after the VDLUFA A 5.1.1, A 6.1.1 and A 6.1.2 standard methods (VDLUFA 1997).

Light conditions

Light penetration in the vegetation was measured in mid of July 2003 at the time of maximum standing crop using SunScan Canopy Analysis System (type SS1, Delta-T Devices Ltd, Cambridge – UK). The probe includes a 1 m light sensitive “wand” containing 64 photodiodes equally spaced along its length and a control sensor. The probe was inserted in the vegetation in a defined height upon the soil surface while the control sensor was installed unshaded above the vegetation. The mean value of photosynthetic active radiation (PAR) in 15 cm height was taken in percent to the full light above the vegetation. This value was considered as light availability for smallgrowing species. Three measurements were performed for the plots of each experimental treatment combination and the mean values of these measurements were used for further analyses.

Soil seed bank

Soil samples for seed bank analysis were taken from each experimental block separately out of the area with and without topsoil removal. Each 960 cm³ sample contained ten 10 cm deep cores taken randomly within the plots using a 3.5 cm diameter corer. The samples were exposed in plastic trays on sterilized soil in an experimental garden for germination. A translucent gauze was used to prevent external seed input. Emerging seedlings were counted and determined regularly over a period of one year.

Data analysis

One-way ANOVAs and Tukey HSD tests with square-root transformed data were performed to study the differences in soil nutrition (N-total, P) between the plots with and without topsoil removal compared to the donor area for the hay material. Differences in the number of seedlings and species emerged out of seed bank samples from plots with and without topsoil removal were analysed using one-way ANOVAs. The dependent variables were square-root transformed to fulfil the ANOVA-assumptions.

Effects of grazing, topsoil removal and hay transfer on light availability at the experimental plots was tested using a three-way ANOVA, fitted to the experimental design.

A Repeated Measurements ANOVA was calculated for the Cumulative Cover (CC) and Cumulative Frequency (CF) of ecological species groups in the four study years. Block was treated as random factor, Grazing (G), Topsoil Removal (R) and Hay transfer (H) – as fixed factors. Error terms for different sources of variation were fitted to the experimental design. Data were $\log(x+1)$ -transformed to fulfil the ANOVA assumptions.

Statistica 6.1 (Statsoft 2004) was used for all analyses.

RESULTS

Site conditions

As a consequence of topsoil removal, a significant reduction of the most important nutrient soil parameters (N: $F = 11.53$, $p < 0.01$ and P: $F = 17.09$, $p < 0.001$) was observed in the study plots (Fig. 2).

Especially the nitrogen values approached the values measured in the soil of the species-rich community of the donor site for hay transfer (Lehmkuhlener Stauung; Tab. 1).

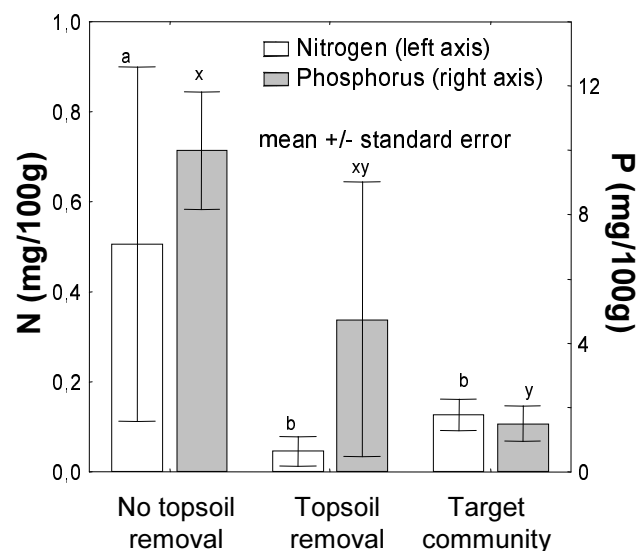


Figure 2. Effects of topsoil removal on the nutrient content in the soil. Non-transformed data of samples taken in 2005 are shown. 1 – Experimental plots without topsoil removal ($n = 4$), 2 – experimental plots with topsoil removal ($n = 4$), 3 – donor site for hay transfer, representative for target community (Lehmkuhlener Stauung; $n = 6$). Significant differences detected by Tukeys HSD-tests ($p < 0.05$) are indicated by different letters.

Two years after applying the treatments, light availability in vegetation differed significantly between the plots with and without topsoil removal (Tukey HSD test $p < 0.05$; Tab. 2; Fig. 3).

Table 1. Differences in nutrient content (squareroot transformed N_{tot} and P) between sites with and without topsoil removal compared to the donor site of hay transfer ("target community"; y = plots with topsoil removal, n = plots without topsoil removal, d = donor site). Results of Tukey-HSD-Tests.

Nutrients/Topsoil removal	N_{tot}	P
y - n	< 0.01	< 0.05
y - d	n.s.	n.s.
n - d	< 0.05	< 0.001

The effects of grazing on light penetration were only significant in plots without topsoil removal (Tab. 2; Fig. 3). Hay transfer had no significant effect on light availability (Tab. 2).

In plots without topsoil removal the groundwater level was on average 20 cm below soil surface without inundation (Tab. 3). At plots, where the upper 30 cm of the soil were removed, differences between the blocks occurred: on the first two blocks the average groundwater level was about 5 - 7 cm below the soil surface and inundation was only observed for short time after heavy raining. Another two blocks were very wet or partly inundated most time during the experiment (Tab. 3).

Table 2. Impact of experimental factors on light availability (PAR%) two years after the start of the experiment. Results of a three-factorial ANOVA.

Effect	F	p
Grazing (G)	1.31	n.s.
Topsoil removal (R)	33.31	< 0.001
Hay transfer (H)	0.24	n.s.
G * R	6.79	< 0.05
R * H	0.46	n.s.
G * R * H	0.06	n.s.

Soil seed bank

The soil seed bank at the study site was represented by 56 species with an average density of 70 000 viable seeds per m². The dominant species *Cirsium palustre*, *Juncus effuses*, *Poa trivialis*, *Ranunculus repens* and *Urtica dioica* amounted to 70 % of the seedlings.

No seedlings of rare or endangered species of fen grassland communities occurred in the soil seed bank samples. The number of seedlings and species differed significantly between plots with and without topsoil removal (seedlings: $F = 80.99$, $p < 0.001$; species: $F = 78.37$, $p < 0.001$; Fig. 4).

Topsoil removal resulted in the reduction of the soil seed bank of more than 95 %.

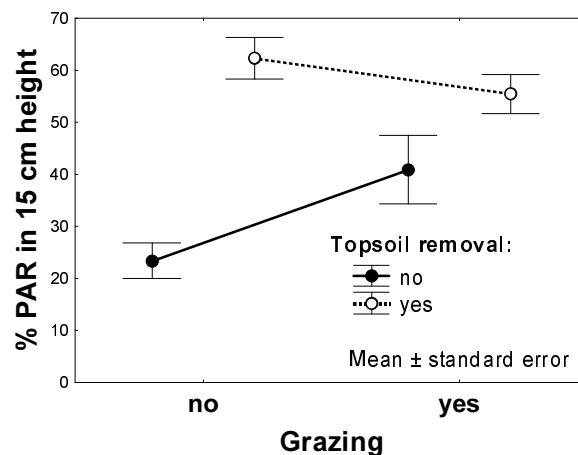


Figure 3. Effects of topsoil removal and moderate grazing on the light availability at the experimental plots two years after starting the three-factorial field experiment.

Effects of grazing, topsoil removal and hay transfer on vegetation development

Altogether 112 plant species were registered in the vegetation relevés of the four experimental blocks. 14 species were definitely transferred with hay material, as there were no other populations of these species in the nearby surrounding and as it is unlikely to expect them to reach the experimental sites in the course of natural dispersal. Another species group containing ten species is marked as probably dispersed by hay material. This includes species, occurring also in the surrounding of the study site with small isolated populations (see Appendix 1). 12 more species are marked as possibly transferred with the hay material due to the results of a preliminary study. These species were common at the study area before the experiment was carried out and thus can not be seen as certainly transferred (Appendix 1).

Table 3. Groundwater level [cm below soil surface] measured monthly at the experimental blocks in 2002-2005.

Block	Topsoil removal	Groundwater level [cm below soil surface]		
		Minimum	Maximum	Mean \pm std. deviation
1	no	-34	-18	-20.54 \pm 7.97
	yes	-11	-4	-7.02 \pm 1.96
2	no	-34	-8	-20.54 \pm 7.97
	yes	-11	5	-5.23 \pm 4.91
3	no	-24	1	-8.27 \pm 7.72
	yes	0	9	4.65 \pm 2.28
4	no	-34	-6	-20.27 \pm 7.82
	yes	-11	7	2.29 \pm 4.76

The largest group of taxa (40 species) were plants, typical for nutrient-enriched agricultural grasslands (Appendix 1). Reed species were represented with 18 taxa, while the target species of moderately used wet hay meadows and of nutrient poor fens and bogs occurred with 15 and 14 taxa respectively. The other 26 taxa were annual and perennial ruderal species, nutrient-rich mud bank community species, hydrophytes and woody species (Appendix 1).

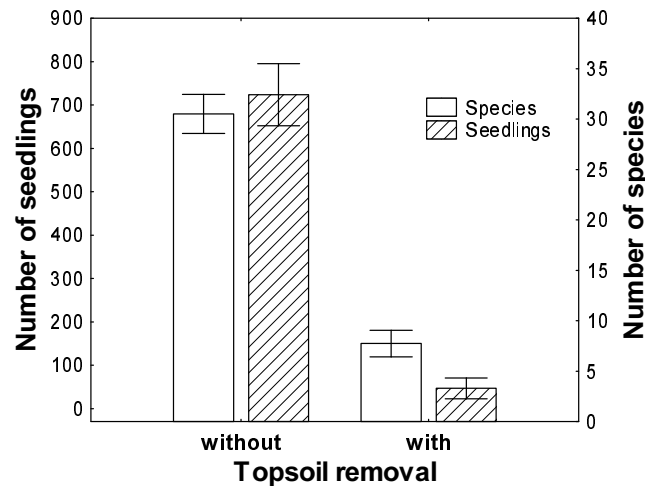


Figure 4. Number of seedlings and species emerged from seed bank samples from plots with and without topsoil removal. Mean and standard error for non-transformed data are shown.

Experimental treatments and their combinations had minor effects on the entire species number. The species number and vegetation cover of plots with removed topsoil and transferred hay material reached a constant value within two years after the start of the experiment. At plots without hay transfer the species number was still increasing after four years of observation and the colonisation of bare soil patches was not fully completed.

For all species groups the factor “time” was significant. While for the most species groups an increase of cumulative frequency and cover was observed during the experiment, species of agricultural grassland (EF) decreased significantly (Tab. 4, Fig 5a,b).

Topsoil removal, hay transfer and especially the combination of these two treatments led to a significant increase of frequency and cover of the target species of nutrient poor fens and bogs (Tab. 4, Fig. 5a,b). Especially small sedges (*Carex echinata*, *Cx. panicea*) and the pioneer *Triglochin palustre* were among the most abundant species. *Triglochin* and *Pedicularis palustris* were most successful in secondary spreading also outside of plots with transferred hay within plots where topsoil was removed (significant time x topsoil removal interaction for species of nutrient poor fens and bogs [SC]). Among the wet meadow species *Cirsium palustre* was abundant at the study site before and during the whole investigation

Table 4. Effects of experimental factors (grazing, topsoil removal, hay transfer) on the Cumulative Frequency (CF) and Cumulative Cover (CC) of different ecological species groups: SC: Species of nutrient poor wetlands (Scheuchzeria-Caricetea community); MO: Species of moderately used wet hay meadows (Molinietalia community); EF: Species of nutrient enriched agricultural grasslands (Eutrophic fen communities: Arrhenateretea and Lolio-Potentillion); PH: Tall-growing reed species (Phragmitetea community); M: miscellaneous ANOVA. Results of a Repeated Measurements ANOVA. Significant effects are shown in bold and marked as follows: * p < 0.05, ** p < 0.01 and *** p < 0.001.

Source of variation	Error	df	CF_SC		CC_SC		CF_MO		CC_MO		CF_PH		CC_PH		CF_EF		CC_EF		CF_M		CC_M	
			MQ	F	MQ	F	MQ	F	MQ	F	MQ	F	MQ	F	MQ	F	MQ	F	MQ	F	MQ	F
Block (B)		3	0.34		0.23		0.14		0.26		2.74		3.82		0.62		1.04		0.08		0.39	
Grazing (G)		1	0.01	0.01	0.01	0.02	1.50	10.81*	0.04	0.15	0.87	0.32	1.05	0.27	1.25	2.01	3.70	3.56	0.09	1.13	0.18	0.46
Topsoil removal (R)		1	19.40	69.34***	8.77	58.84***	4.96	8.06	9.88	32.80**	0.01	0.02	0.004	0.004	2.84	45.57***	6.70	19.99***	0.08	2.00	0.24	1.59
	B*G	3	0.28		0.15		0.62		0.30		0.36		1.08		0.06		0.33		0.04		0.15	
	R*G	1	0.02	0.08	0.01	0.05	0.94	2.25	3.01	10.86*	0.60	3.40	0.31	0.65	0.19	0.96	0.02	0.03	0.36	12.98*	0.91	2.40
Hay transfer (H)		1	6.23	23.68***	4.27	29.21***	0.24	0.58	0.13	0.45	0.12	0.68	0.34	0.72	0.05	0.27	0.07	0.12	0.08	3.01	0.42	1.10
	B*G*R	3	0.26		0.15		0.42		0.28		0.18		0.48		0.20		0.55		0.03		0.38	
	R*H	1	5.81	70.39***	4.13	203.80***	0.01	0.11	0.01	0.12	0.01	0.09	0.01	0.01	0.05	0.23	0.29	1.02	0	0	0.01	0.02
	G*H	1	0.05	0.63	0.01	0.60	0.50	5.12	0.08	0.66	0.02	0.16	0.76	1.27	0.07	0.37	0.04	0.14	0.16	4.43	0.10	0.23
	R*H*G	1	0.04	0.52	0.01	0.65	1.16	11.92*	1.08	9.04*	0.29	2.95	3.29	5.50	0.92	4.75	0.95	3.30	0.05	1.33	0.01	0.02
	B*G*R*H	3	0.08		0.02		0.10		0.12		0.10		0.60		0.19		0.29		0.04		0.45	
Time (T)		3	0.17	6.65***	0.19	8.77***	0.54	15.32***	1.05	18.43***	1.85	70.57***	4.55	110.24***	0.25	9.84***	0.44	8.03***	0.18	11.47***	0.04	0.29
	T*G	3	0.01	6.56***	0.02	8.31***	0.06	9.50***	0.13	2.89*	0.04	14.34***	0.02	31.09***	0.01	11.14***	0.15	20.80***	0.03	0.58	0.13	9.11***
	T*R	3	0.17	0.30	0.18	5.29**	0.33	0.17	0.16	0.22	0.37	0.15	1.28	0.47	0.28	0.47	1.13	0.49	0.01	1.83	1.21	0.73
	T*H	3	0.01	0.49	0.12	0.87	0.01	1.79	0.01	2.32	0.01	1.57	0.02	0.46	0.01	0.62	0.03	2.69	0.03	1.65	0.10	0.95
	T*G*R	3	0.02	0.75	0.03	4.53**	0.03	0.67	0.10	0.69	0.06	0.12	0.10	0.01	0.06	0.35	0.06	0.13	0.03	0.21	0.14	0.13
	T*R*H	3	0.02	0.64	0.10	1.23	0.02	0.89	0.04	1.79	0.01	2.41	0.0004	2.49	0.01	2.20	0.01	1.02	0.003	1.86	0.02	1.03
	T*G*H	3	0.01	0.56	0.02	0.93	0.02	0.51	0.02	0.30	0.01	0.20	0.02	0.37	0.01	0.55	0.03	0.61	0.01	0.82	0.06	0.46
	T*G*R*H	3	0.03	1.07	0.03	1.22	0.01	0.25	0.03	0.51	0.01	0.03	0.02	0.57	0.003	0.12	0.14	2.53	0.003	0.20	0.03	0.26
Residual		72	0.03		0.02		0.04		0.06		0.03		0.04		0.03		0.05		0.02		0.13	

period, the abundance of *Caltha palustris* and *Silene flos-cuculi* increased at plots with hay transfer while *Lotus pedunculatus* and *Myosotis scorpioides* became frequent especially on plots with topsoil removal.

In contrast, frequency and cover of species of agricultural grassland (EF) was significantly reduced by topsoil removal in comparison to the undisturbed plots (Fig. 5a, b).

Most species transferred with the hay, were only present in areas with removed topsoil. The main exception was the establishment of the hemiparasitic herb *Rhinanthus angustifolius* in plots with intact topsoil.

While the number and cover of target species had already reached their maximum in the second year of the experiment in case of topsoil removal and hay transfer, they increased slowly during the four years of observation in the areas with topsoil removal but without addition of hay.

The effects of grazing were of minor importance for species composition and vegetation cover. However, for wet meadow species grazing led to a significant increase of cumulative frequency (Tab 4, Fig. 5a). This was also the case for the interaction of time and grazing for all species groups. Furthermore, the interaction of topsoil removal and grazing was significant: grazing had a positive effect on the cumulative cover of wet meadow species, when topsoil was removed (Tab. 4, Fig. 5b).

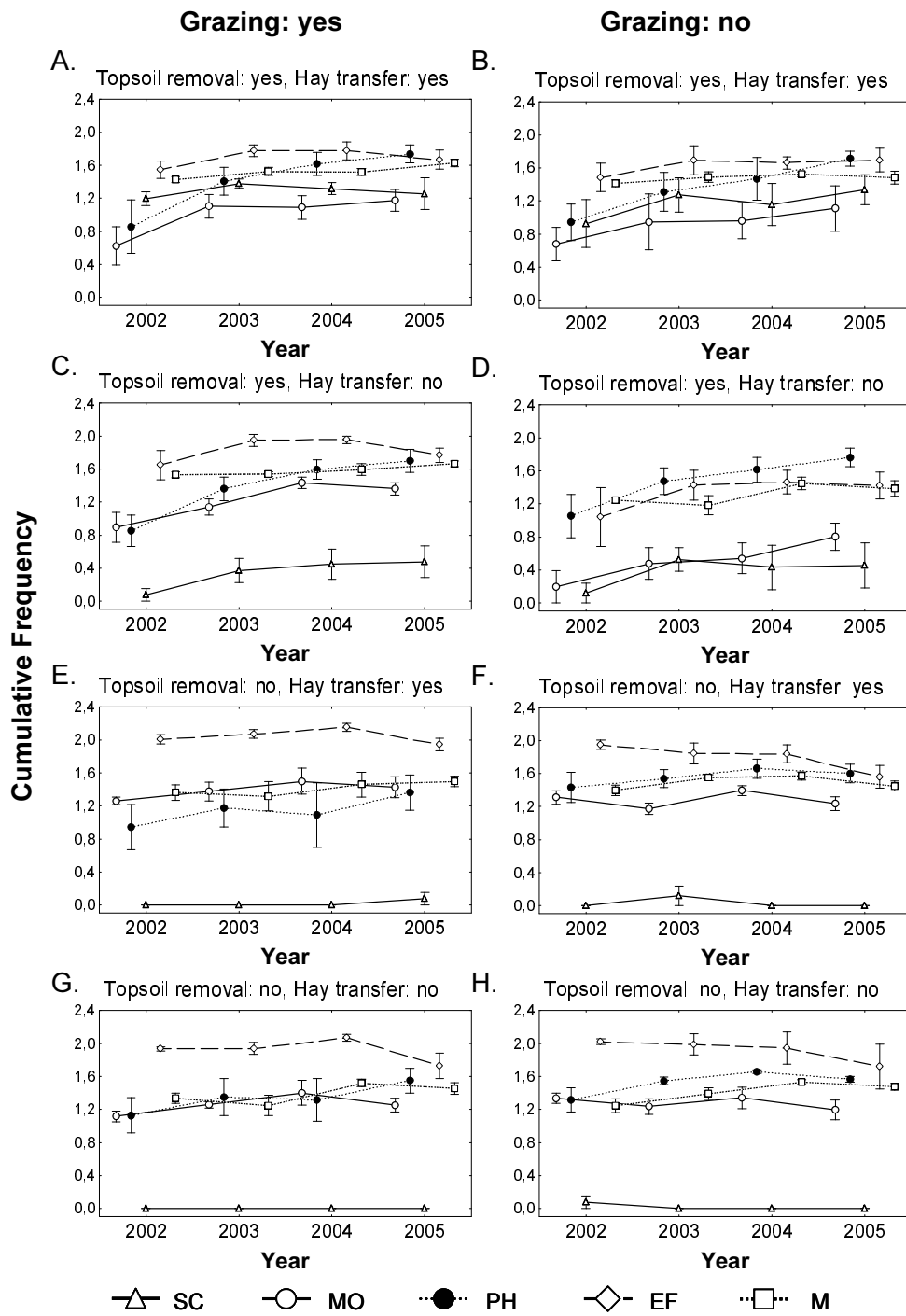
In some cases the onward colonisation of the area by reed species (PH) was also suppressed by grazing, while species of agricultural grassland (EF) occurred with higher frequency and cover in grazed plots during the time of observation (significant time/grazing interaction, Tab. 4, Fig. 5a, b).

DISCUSSION

Nutrient reduction

A reduction of soil fertility by topsoil removal could be confirmed by our results. The values for nitrogen and phosphorus in the soil after the removal of the upper peat layer, which was most mineralised and eutrophic, were reduced to the level of our target community. This effect of topsoil removal has also been documented by Hölzel & Otte (2003) and Patzelt et al. (2001). We did not analyse the effects of grazing on soil nutrient content in our experiment, as in general effects of grazing on soil fertility can be observed only after longer time periods (e.g. Bakker 1989). Nevertheless, grazing may have an additional stabilizing effect on soil nutrients after the reduction due to topsoil removal. Stammel et al. (2003) showed that species richness and vegetation structure on a nutrient poor fen site can be preserved by moderate grazing.

a.



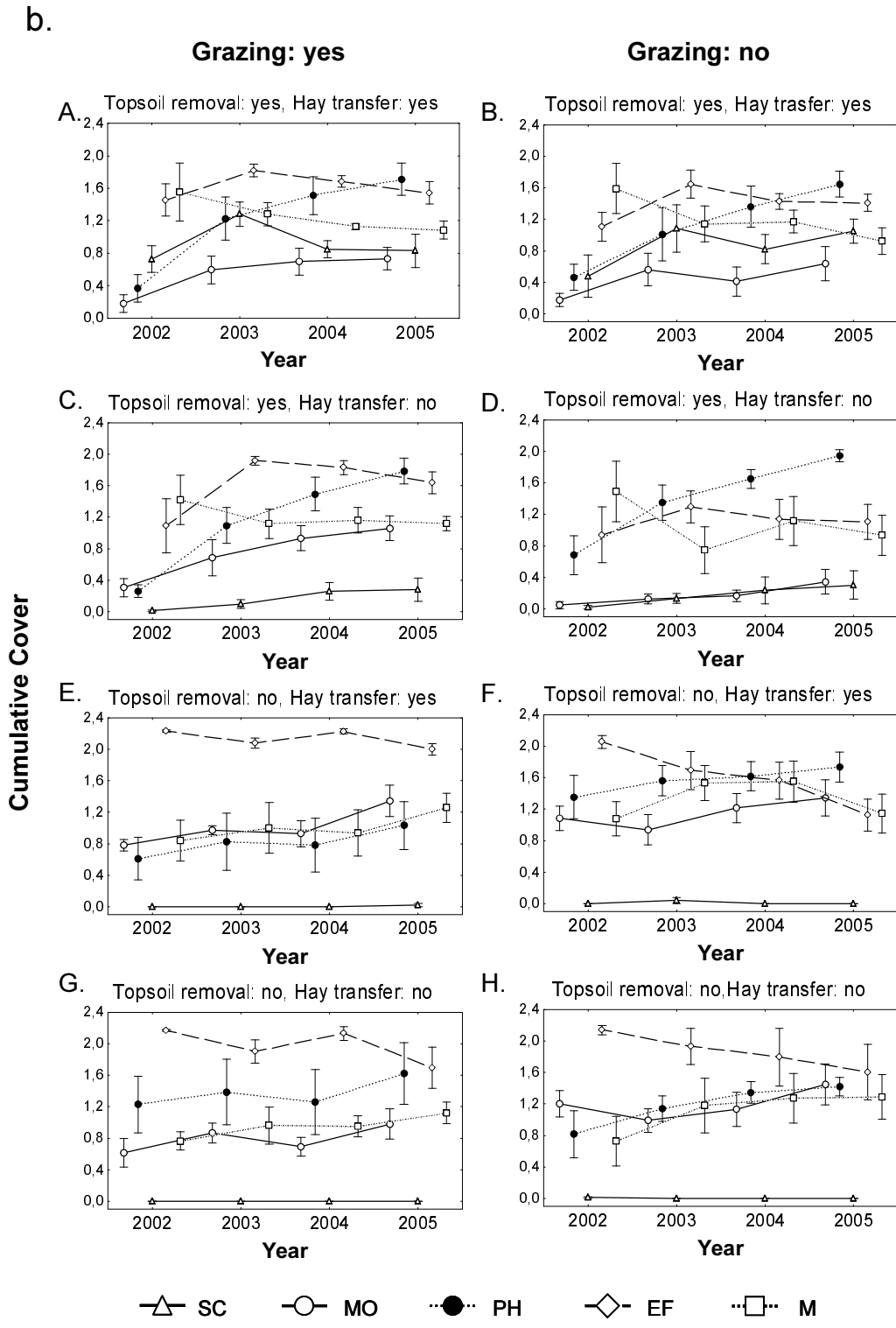


Figure 5. Log (x+1)-transformed cumulative frequency (a) and cumulative cover (b) of species groups (SC - Species of nutrient poor fens and bogs, MO - Species of moderately used wet hay meadows, EF - Species of nutrient enriched agricultural grasslands, PH - Tall-growing reed species, M - Miscellaneous) recorded during four years of observation (2002 - 2005) at plots of the three-factorial experiment with the factors grazing, topsoil removal and hay transfer. Mean and standard error are presented.

Changes in species composition and dominance

In general, plant species composition is the result of interactions between seed availability in soil seed banks and seed rain, edaphic and climatic conditions as well as disturbance and competition (e.g. Tilman 1988, Bakker et al. 1996).

For most formerly extensively used or abandoned fen grasslands, the soil seed bank is considered to be irrelevant for restoring species diversity, as it is dominated by species of agricultural grasslands and ruderals (McDonald et al. 1996). Mostly “target”-species are absent (van Andel et al. 1993, Blomqvist et al. 2003) or present only in small numbers, insufficient for restoration (Hölzel & Otte 2004). Although, Jensen (2004) had shown recently a high potential for long-term persistent seed banks in fen species, the removal of soil seed bank is still thought to be an important step in fen grassland management (Ramseier, 2000). Our own analysis of the seed bank at our investigation site confirmed the assumption, that the soil seed bank could not increase species diversity at this site, because the great majority of seedlings emerged from the soil samples belong to a few highly competitive species (e.g. *Urtica dioica*). The comparison between seed bank samples of plots with and without topsoil removal showed, that topsoil removal eliminated the seed bank successfully.

Another important effect of topsoil removal is the simultaneous displacement of resident competitors and the creation of patches of bare soil. This results in the creation of suitable gaps for germination and establishment for many low competitive species (van Diggelen et al. 1997, Ramseier 2000, Verhagen et al. 2001). In our study, dispersal limitation for these species was abolished by means of hay transfer.

Even after the applied treatments of the experiment, plots with topsoil removal and hay transfer were in most cases colonised by dominant species of the nearer surrounding within a short time. Especially reed species with clonal growth, building long tillers (e.g. *Carex acutiformis*), successfully colonised the plots. The increase of reed species, observed at plots with topsoil removal during the period of four investigation years is an illustration of this effect. Furthermore, the seed rain of the surrounding played an important role for vegetation development. The seed rain of species resident in the area (approx. 57 000 seeds /m²; Jensen 1998) is much higher than the amount of seeds of target species, brought with hay material (2 000-12 000 seeds/m²; Rasran et al. 2006).

The experimental blocks were comparatively small patches, surrounded by well developed current vegetation of abandoned fens. This promoted a rapid colonisation of the newly created open patches by species of eutrophic fens from the nearer surrounding. Similar observations were made also by Patzelt (1998). This effect could be minimized by applying the treatments at larger scales.

Grazing is known to suppress the natural succession in grassland ecosystems and changing the competitive interactions in favour of smaller, stress-tolerant species (e.g. Stammel et al. 2003, Hellström et al. 2003).

In our case effects of grazing on the colonisation of the plots during the period of investigation (time x grazing interaction) were observed for almost all regarded species groups. We expect grazing to play a major role in the long-term development of the area by creating gaps for germination, suppressing the dominant vegetation or as dispersal vector (e.g. Bakker 1989, Bullock et al. 1994, Couvreur et al. 2004).

Establishment of target species

From the 41 species expected to be found in the hay material of the evaluated donor site (Rasran et al. 2006) 33 (80%) were observed on the experimental plots. Similar transfer rates were achieved also by Hölzel & Otte (2003). Nonetheless, the real impact of hay transfer on species diversity is presumably lower, due to the fact that some of these species are common in the landscape and were already present in the surrounding vegetation of the experimental site before hay transfer. In contrast, for the target species, which were not or only sporadically present in the study area, the transfer rate of 78 % compared to donor site is considered to be realistic (compare Patzelt et al. 2001). Especially germination and establishment of small sedges was high in many cases in spite of poor regeneration by seeds of many species of this genus described in literature (e.g. Schütz 2000). This can be taken as evidence for the successful restoration. Among the target species, present on the donor site but failed to establish on the experimental plots, *Carex dioica* should be mentioned as an example for a species with low seed production and poor regeneration with generative diaspores. Other species like *Viola palustris* and *Parnassia palustris* released their seeds earlier or later than the time, at which the hay material for transfer was gathered. Thus, they could not be transferred with the hay.

All species, transferred with the hay material, are dependent on the quality of the substrate and availability of safe sites (Kirmer & Mahn 1996). We assume that on plots without topsoil removal, the number and quality of gaps was insufficient for most of our target species, as these species occurred only on plots with topsoil removal. The main exception was *Rhinanthus angustifolius*, which germinated and established similarly on plots with and without topsoil removal. *Rhinanthus* spp. are known to be comparatively strong competitors, able to germinate in dense vegetation due to their relatively large seeds (van Hulst et al.

1987). As hemiparasites they profit from the plants of their surrounding and occur in high individual numbers even in abandoned grasslands (de Hullu 1985).

For other target species (especially for species of nutrient poor fens and bogs) the areas with topsoil removal possessed the most appropriate conditions for establishment: patches of bare soil and reduced competition, reduced soil nutrition and raised groundwater levels (Stockey & Hunt 1994, Ramseier 2000, Jansen et al. 2004). Though, the last mentioned factor appeared to be problematic, as it led to temporary inundations at two of the four experimental blocks. Successful establishment of wet meadow species can be hampered by long term inundation (Jansen & Roelofs 1996).

After two years of succession plots with topsoil removal were still not fully covered by vegetation, so that enough gaps for further colonisation remained at the plots. This led to successful secondary dispersal events of target species from plots with transfer of hay material to plots without hay transfer (see also Hölzel & Otte 2003). This confirms our assumption that plots with hay transfer can function as initials for further colonisation by target species.

As grazing had a significant effect on the frequency of wet meadow species, we assume an increase of the number of available gaps for the establishment of these species and a shift in the competitive conditions at the site to their advantage (compare Stammel et al. 2003).

CONCLUSIONS

We conclude, that topsoil removal lead to a reduction of nutrients to the level of target communities. Further, the removal of highly competitive species and their seed bank could be achieved. Dispersal limitation of rare or endangered plant species was abolished by the means of transfer of seed-rich hay material. The combination of both factors led to the successful establishment of the highest number of target species. The effect of moderate grazing on species diversity was less clear, but we consider it to be important in a long term.

For further application in fen grassland restoration we recommend additionally to a moderate form of continuous management (grazing/cutting), a combination of topsoil removal and hay transfer preferably at large scales to minimize edge-effects.

Appendix. Plant species, occurring at the experimental plots during the four years of investigation. § - Species, present with their propagules in hay material (see also Rasran et al. 2006). ! - species, which are concluded to be definitely transferred with the hay material, as there are no other populations of these species in the nearby surrounding and it is unlikely to expect them to reach the experimental sites in the course of natural dispersal. ? - species, probably dispersed with hay material while their occurrence in experimental plots could also be explained by other reasons, but the origin of seeds out of hay is still the most presumable one. Key of species groups: SC: Species of nutrient poor fens and bogs (Scheuchzerio-Caricetea community); MO: Species of moderately used wet hay meadows (Molinietalia community); EF: Species of nutrient enriched agricultural grasslands (Eutrophic fen communities: Arrhenateretea and Lolio-Potentillion); PH: Tall-growing reed species (Phragmitetea community); M: Annual and perennial ruderal species, nutrient-rich mud bank community species and miscellaneous, e.g Salix spp.. *** - abundant (occurring in more than 10% of relevés / amounting to > 10 % of all seedlings emerged from seed bank samples), ** - common (1-10%), * - rare (less than 1%).

Species group	Occurrence out of hay	Species	Associated with:								Occurrence in seed bank		
			Topsoil removal	yes	yes	no	no	yes	yes	no	no	with topsoil	without topsoil
			Hay transfer	yes	no	yes	no	yes	no	yes	no		
			Grazing	yes	yes	yes	yes	no	no	no	no		
SC	! §	<i>Agrostis canina</i> L.		***	**			***	**				
SC	! §	<i>Briza media</i> L.		**				*					
SC	! §	<i>Carex echinata</i> Murray		***	**			***	**				
SC	! §	<i>Carex flava</i> agg. c.f. <i>demissa</i>						*					
SC	? §	<i>Carex nigra</i> (L.) Reichard		**		*		**					
SC	! §	<i>Carex panicea</i> L.		***	*			**					
SC	! §	<i>Eriophorum angustifolium</i> Honck.						**					
SC	.	<i>Juncus subnodulosus</i> Schrank						**					
SC	! §	<i>Menyanthes trifoliata</i> L.						**			*		
SC	! §	<i>Pedicularis palustris</i> L.			**			**	**				
SC	! §	<i>Potentilla erecta</i> (L.) Raeusch.		**						*			
SC	! §	<i>Potentilla palustris</i> (L.) Scop.						*					
SC	!	<i>Sagina nodosa</i> (L.) Fenzl						**					
SC	! §	<i>Triglochin palustre</i> L.		**	**			***	**				
MO	? §	<i>Caltha palustris</i> L.		***		**		***		***	**		
MO	?	<i>Carex ovalis</i> Good.		*				*					
MO	.	<i>Cirsium oleracium</i> (L.) Scop.		*		**							
MO	§	<i>Cirsium palustre</i> (L.) Scop.		***	***	***	***	***	**	***	***	***	***
MO	§	<i>Filipendula ulmaria</i> (L.) Maxim.			*	**			*	**			
MO	.	<i>Lotus pedunculatus</i> Cav.		*	**	**	**	**	**			*	
MO	§	<i>Lythrum salicaria</i> L.						*					
MO	.	<i>Myosotis scorpioides</i> L.		**	***	***	**	**	**	**	**	*	
MO	? §	<i>Ranunculus flammula</i> L.		*	*	*	*	**	**	*	*		
MO	! §	<i>Rhinanthus angustifolius</i> C. C. Gmel.		**		**		**		**			
MO	.	<i>Scirpus sylvaticus</i> L.		**				**					
MO	? §	<i>Scutellaria galericulata</i> L.		**		*	**	***		*			
MO	? §	<i>Silene flos-cuculi</i> (L.) Clairv.		**	*			**		**	**		
MO	.	<i>Stellaria alsine</i> Grimm		**	***	**	**			**	**	***	*
MO	.	<i>Valeriana officinalis</i> agg.								**	*		
EF	.	<i>Agrostis stolonifera</i> agg.		**	**	***	**	***	**	**	**	**	**
EF	.	<i>Ajuga reptans</i> L.				**	**			**	**	*	
EF	.	<i>Alopecurus geniculatus</i> L.		***	***	***	***	**	**	*	*	**	*
EF	.	<i>Alopecurus pratensis</i> L.			*	***	***	*		***	**	*	
EF	§	<i>Anthoxanthum odoratum</i> agg.		**	**	***	***	**		***	***	*	
EF	.	<i>Anthriscus sylvestris</i> (L.) Hoffm.				**	*						
EF	.	<i>Cardamine pratensis</i> agg.		**	**	**	**	**	**	**	**	**	*
EF	.	<i>Carex hirta</i> L.						**	**				
EF	§	<i>Cerastium holosteoides</i> Fr.		**	**	***	***	**	**	***	***	**	*
EF	.	<i>Cynosurus cristatus</i> L.				*							
EF	.	<i>Dactylis glomerata</i> agg.					*						
EF	.	<i>Deschampsia cespitosa</i> agg.				*						*	*
EF	.	<i>Festuca pratensis</i> Huds. s. l.				*	**	*		*	**		
EF	? §	<i>Festuca rubra</i> agg.		***				***		**	**	*	
EF	.	<i>Galium mollugo</i> agg.				*							
EF	.	<i>Glechoma hederacea</i> L.			*	*	**			**	**	*	
EF	.	<i>Glyceria fluitans</i> agg.		***	***	***	***	***	***	***	***	**	*
EF	§	<i>Holcus lanatus</i> L.		***	***	***	***	***	**	***	***	**	*
EF	.	<i>Holcus mollis</i> L.								**	**		

Appendix. (continued)

Species group	Occurrence out of hay	Species	Associated with:										Occurrence in seed bank	
			Topsoil removal		yes		no		yes		no		with topsoil	without topsoil
			yes	no	yes	no	yes	no	yes	no				
EF	? §	<i>Juncus articulatus</i> L.	***	***	**	**	***	***	**	**	**	**	.	
EF	.	<i>Juncus bufonius</i> agg.	*	*	.	
EF	.	<i>Juncus effusus</i> L.	***	***	***	***	***	**	***	***	***	***	*	
EF	.	<i>Lathyrus pratensis</i> L.	.	.	*	**	**	.	.	
EF	.	<i>Lolium perenne</i> L.	.	*	**	**	*	*	.	
EF	! §	<i>Luzula multiflora</i> (Ehrh.) Lej. s. str.	*	.	.	.	*	
EF	.	<i>Persicaria hydropiper</i> (L.) Delarbre	**	.	*	
EF	? §	<i>Plantago lanceolata</i> L.	.	.	**	**	**	.	**	.	**	.	.	
EF	.	<i>Plantago major</i> L.	.	.	*	*	*	*	.	
EF	.	<i>Poa pratensis</i> agg.	*	*	.	
EF	.	<i>Poa trivialis</i> agg.	***	***	***	***	***	***	***	***	***	***	*	
EF	§	<i>Ranunculus acris</i> L.	**	**	**	**	**	*	**	***	**	*	.	
EF	.	<i>Ranunculus repens</i> L.	***	***	***	***	**	***	***	***	***	***	*	
EF	§	<i>Rumex acetosa</i> L.	**	***	***	***	**	**	***	***	***	**	.	
EF	.	<i>Rumex crispus</i> L.	**	**	***	***	*	**	***	**	*	*	.	
EF	.	<i>Rumex obtusifolius</i> agg.	.	.	**	**	.	.	**	*	*	*	.	
EF	.	<i>Taraxacum officinale</i> agg.	**	**	**	**	*	.	*	**	**	**	*	
EF	.	<i>Trifolium pratense</i> L.	.	**	*	
EF	§	<i>Trifolium repens</i> L.	*	**	**	*	**	.	.	.	**	.	.	
EF	.	<i>Veronica chamaedrys</i> L.	.	.	.	*	.	.	**	
EF	.	<i>Veronica serpyllifolia</i> L.	.	**	**	*	*	.	*	*	*	**	.	
PH	.	<i>Berula erecta</i> (Huds.) Coville	**	**	
PH	.	<i>Carex acutiformis</i> Ehrh.	**	***	**	***	***	***	**	***	***	.	.	
PH	.	<i>Carex acuta</i> L.	*	**	**	.	.	.	
PH	.	<i>Carex paniculata</i> L.	**	.	.	.	**	.	*	
PH	.	<i>Carex vesicaria</i> L.	.	*	
PH	.	<i>Equisetum fluviatile</i> L.	***	***	**	**	***	***	***	***	***	.	.	
PH	.	<i>Equisetum palustre</i> L.	***	***	**	**	***	***	***	***	***	.	.	
PH	.	<i>Eupatorium cannabinum</i> L.	***	***	**	**	**	**	**	.	.	*	.	
PH	§	<i>Galium palustre</i> L.	**	**	***	***	**	**	***	***	***	**	.	
PH	.	<i>Glyceria maxima</i> (Hartm.) Holmb.	**	**	**	**	**	**	**	**	**	.	.	
PH	.	<i>Lysimachia nummularia</i> L.	.	.	**	**	.	.	.	**	.	.	.	
PH	.	<i>Lysimachia vulgaris</i> L.	**	*	.	
PH	§	<i>Mentha aquatica</i> L.	**	***	**	**	**	**	**	**	**	*	.	
PH	.	<i>Phalaris arundinacea</i> L.	**	.	*	***	*	**	**	**	**	*	.	
PH	.	<i>Rumex hydrolapathum</i> Huds.	**	*	.	**	.	*	*	
PH	.	<i>Schoenoplectus lacustris</i> (L.) Palla	**	
PH	.	<i>Sparganium erectum</i> L.	***	**	**	***	**	***	***	***	**	.	.	
PH	.	<i>Typha latifolia</i> L.	***	***	.	.	***	**	
M	.	<i>Alnus glutinosa</i> (L.) P.Gaertn., juv.	**	***	**	*	**	*	
M	.	<i>Callitriche</i> sp.	*	
M	.	<i>Cardamine amara</i> L.	**	**	**	**	**	**	**	**	**	**	.	
M	.	<i>Cirsium arvense</i> (L.) Scop.	.	.	**	**	
M	.	<i>Eleocharis palustris</i> agg.	*	**	
M	.	<i>Elymus repens</i> (L.) Gould.	.	*	**	**	.	.	.	**	*	*	.	
M	? §	<i>Epilobium ciliatum</i> Raf.	**	*	.	.	**	*	.	
M	.	<i>Epilobium hirsutum</i> L.	***	***	**	**	**	**	**	**	**	*	.	
M	.	<i>Epilobium tetragonum</i> L.	**	**	**	**	**	*	**	**	**	**	*	
M	.	<i>Epilobium palustre</i> L.	**	**	.	.	**	**	.	
M	.	<i>Epilobium</i> sp.	***	***	***	***	**	***	***	***	***	.	.	
M	.	<i>Galeopsis tetrahit</i> agg.	**	*	**	***	.	.	**	***	***	.	.	
M	.	<i>Galium aparine</i> agg.	.	.	**	**	**	.	**	**	*	.	.	
M	.	<i>Lamium album</i> L.	.	.	**	**	.	.	**	.	.	*	.	
M	.	<i>Lemna minor</i> L.	***	***	*	.	***	***	
M	.	<i>Lemna trisulca</i> L.	**	**	
M	.	<i>Persicaria lapatifolia</i> (L.) Delarbre	.	.	.	*	
M	.	<i>Ranunculus aquatilis</i> agg.	**	
M	.	<i>Ranunculus sceleratus</i> L.	*	
M	.	<i>Salix</i> sp. juv.	**	***	.	.	**	**	
M	.	<i>Sonchus asper</i> (L.) Hill	.	*	
M	.	<i>Spirodella polyrhiza</i> (L.) Schleid.	.	*	.	.	.	**	
M	.	<i>Stellaria media</i> agg.	.	.	**	*	.	.	*	.	*	.	.	
M	.	<i>Tussilago farfara</i> L.	**	**	.	.	**	
M	.	<i>Urtica dioica</i> L.	**	*	***	***	**	.	***	***	***	***	*	
M	.	<i>Veronica arvensis</i> L.	.	.	**	**	
M	.	<i>Veronica beccabunga</i> L.	.	**	

Plate IV



Picture 8. Installation of the three-factorial field experiment in August 2001: top soil removal.



Picture 9. Plot with moderate grazing, topsoil removal and hay transfer of the three-factorial field experiment with fruiting *Eriophorum angustifolium* Honck. and flowering *Pedicularis palustris* L. individuals in June 2005.

General conclusions

This thesis has confirmed the assumption, that target species of fen grassland restoration are in many cases seed- and (or) microsite-limited. For achieving restoration success, the abolition of these limitations is as important as the restoration of the appropriate habitat conditions.

To abolish microsite-limitation, an installation of moderate grazing or cutting is a widely accepted method for different types of grasslands (see e.g. Stammel 2003). This is also the case for fen grasslands, where high species diversity has developed under the conditions of continuous landuse in Central Europe during the last millennia.

In highly degraded fen grasslands in which soil structure have been altered due to drainage and nutrient availability is much higher than in semi-natural systems, moderate landuse may not be sufficient to create appropriate site conditions for the mostly weak competitive rare or endangered target species. In such cases, topsoil removal might be the matter of choice, as it restores both the site conditions (hydrology, nutrient status) and removes the original vegetation together with its seed bank. Additionally patches of bare soil are provided, which are considered as appropriate microsites for germination and establishment of target species.

Although several endangered fen grassland species can survive for many years in form of long-term persistent seed banks in the soil (see e.g. Jensen 2004) and dispersal of endangered species can not be excluded (see e.g. Vogt et al. 2004), colonisation of restoration sites in riparian fens via natural dispersal processes is unlikely as a consequence of the restricted number of the diaspores of these target species in the landscape and the high stochasticity of dispersal and establishment processes. This explains the long periods of time, which are often necessary for the establishment of species-rich communities after improving the site conditions by restoration measures. A rapid restoration of species diversity is only possible, if seed limitation is overcome by directed introduction of viable diaspores. Hay transfer is a promising method of plant species introduction especially if an appropriate donor site was chosen.

Based on the data of this thesis a combination of two initial measures (topsoil removal, hay transfer) together with continuous moderate management (grazing/cutting) can be recommended for future restoration projects in fen grasslands.

Knowledge of factors limiting species diversity is important both regarding the theoretical aspects of population and community ecology and the planning of management for nature conservation. Even in such a well investigated ecosystem type, as riparian fen grasslands, a significant lack of information still exists. The intention of the present thesis is to extend the knowledge to seed- and microsite-limitation in fen grasslands, though, further studies on this subject are necessary.

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Summary

The present study was set up to investigate the mechanisms limiting plant populations and species diversity in fen grasslands and to test, if management measures, proposed for fen restoration are able to overcome these limitations.

As the main limitation types seed limitation and microsite- (gap-) limitation were regarded. Additionally interactions of these limitations with site conditions (productivity) were investigated. As restoration measures, different ways of species reintroduction (sowing, transplanting, transfer of seed-rich hay material) and of site management (moderate grazing, mowing, litter removal, gap creation, topsoil removal) were studied.

SEED- AND MICROSITE- LIMITATION

The factors limiting colonisation for the two endangered hemiparasitic fen-grassland species *Pedicularis palustris* L. and *Rhinanthus angustifolius* C. C. Gmel. were analysed by means of a factorial field experiment. The species were sown with three different densities (250, 1 250 and 5 000 seeds/m²) in plots with different intensities of disturbance (undisturbed control, mowing, small and large gaps).

Both studied species were seed-limited: with increasing sowing density, seedling recruitment grew tenfold (from 37 to 370 individuals per m²) for *Pedicularis* and 15-fold (from 37 to 560 individuals per m²) for *Rhinanthus*. In addition, establishment success and fruit production per plot increased with sowing density. Nevertheless, seedling survival in relation to initial sowing density was significantly (about 50%) lower at the highest sowing density when compared to the other sowing treatments for both species. The studied species differed in their reaction to disturbance: *Pedicularis* was found to be dependent upon gaps for successful establishment (six-fold less established individuals without experimentally created gaps), while nearly the same numbers of individuals of *Rhinanthus* occurred in all disturbance treatments, including the undisturbed control.

It can be concluded that the two species studied differ in their reaction to disturbance treatments, as disturbance influenced the availability of microsites for them in a different way. The larger seeded *Rhinanthus* was able to establish populations after sowing independent of disturbance and thus was not microsite-limited, while *Pedicularis* (a weak competitor with smaller seeds) needed gaps for germination and establishment and thus was microsite-

limited. Additionally, both species were seed-limited, as higher sowing densities resulted in higher numbers of plants in all treatments.

EFFECTS OF LITTER REMOVAL AND MOWING

To study the interactions between site productivity and factors limiting plant populations the effects of mowing and litter removal on germination, growth and establishment of two common fen grassland species (*Silene flos-cuculi* (L.) Clairv. and *Lotus pedunculatus* Cav.) were analysed in a factorial field experiment along a site productivity gradient. Seeds (3 200 per m²) and transplants (four juvenile individuals per 0.0625 m² plot) of both study species were added to plots with different combinations of the two factors (litter removal: yes/no; mowing: yes/no). The experiment was situated at seven fen grassland sites in Northern Germany differing in nutrient availability, vegetation composition and standing crop.

For both species, positive effects of mowing and litter removal on the numbers of germinated seeds were registered. Additionally, the relative importance of mowing and litter removal for germination and establishment differed along the productivity gradient: The effect of litter removal was mostly significant at sites with a low nutrient availability and standing crop while the effect of mowing was more important at sites with higher productivity.

The results of the experiment confirm the assumption that the relative importance of single limiting factors and effects of different management types can shift along a productivity gradient.

SEED CONTENT OF HAY

The applicability of hay material as source of plant diaspores for the restoration of species-rich fen grasslands was examined by collecting hay material, recording vegetation composition and analysing seed production at five regularly mown species-rich fen sites in Northern Germany. The seed content in the hay was determined and compared with the vegetation to analyse, how the seed content of the hay reflected the species in the vegetation. For choosing the site with the highest content of seeds of regionally rare and characteristic fen grassland species in the hay a rarity-weighted fen grassland species score was calculated for all investigated sites.

The amount of species represented as seeds in the hay material in comparison to aboveground vegetation was between 40% and 70% for the different sites. A cluster analysis showed a high similarity between aboveground vegetation and hay material, especially for one particular site. The number of seeds in hay material ranged from about 2 000 to 12 000

per square metre. The viability of the seeds of herbs and sedges was high (approximately 80%) whereas the viability of grasses was only about 40%. Germination percentage was much lower for herbs, sedges and grasses (20-50%), which probably was caused by dormancy of the seeds.

Based on the rarity-weighted fen grassland species score of the hays' seed content, and of the relation between aboveground vegetation and species composition of the hay one particular site (low productive sedge-dominated fen meadow) was chosen as a donor site for hay transfer, even though the entire seed production per square metre in this community was comparatively low.

RESTORATION OF RIPARIAN FEN GRASSLANDS

Hay from the species-rich donor site, evaluated after the abovementioned study was used for a restoration experiment aiming to increase species diversity of a eutrophic fen grassland in the Upper Eider Valley. Besides hay transfer, the effects of topsoil removal and moderate grazing on vegetation were studied in a three-factorial field experiment with four replicats and eight treatment combinations (at plots á 5 x 5 m). The experiment was established removing topsoil to a depth of 30 cm, transferring hay at a ratio of 1:1 to the donor site and excluding grazing via fencing following the respective treatment combinations in autumn 2001. Soil nutrients and seed bank were analysed at the beginning of the experiment while species composition and vegetation development was monitored during four years (2002-2005).

Topsoil removal had a significant effect on the abundance of different plant species groups: resident vegetation of agricultural grasslands was suppressed, while clonal growing reed species were in advantage in recolonising the area. The establishment of regionally rare and endangered species of nutrient poor fens and wet meadows out of hay was achieved mainly on plots with topsoil removal, with the exception of *Rhinanthus angustifolius*, which also established on plots with intact topsoil. Effects of grazing after four years of the experiment were of minor importance for species composition, but an increase of cover of typical wet meadow species was recorded.

The establishment of target plant species of nutrient poor fens was most successful when both the adequate number of viable diaspores and suitable sites for germination and establishment were available. Size, number and quality of gaps differ for each species dependent on current management, disturbance and nutrient status of the site. In the experiment, a significant number of suitable gaps for germination and establishment was met by target species of nutrient poor fens and wet meadows after topsoil removal. Hay transfer

was an appropriate source for viable seeds. A combination of these two initial measures together with continuous moderate management (grazing/cutting) can be recommended for further restoration in fen grasslands.

CONCLUSIONS

This thesis has confirmed the assumption, that target species of fen grassland restoration are in many cases seed- and (or) microsite- limited. Thus, a rapid restoration of species diversity is only possible if these limitations are overcome by an introduction of viable diaspores and the creation of a sufficient number of gaps.

Plate V



Picture 10. Moderately grazed fen site in the Upper Eider Valley (May 2002).



Picture 11. Moderately grazed eutrophic fen site in the Upper Eider Valley (site of the three-factorial field experiment; August 2001).

Zusammenfassung

Das Ziel der vorliegenden Arbeit ist es, Mechanismen, die Pflanzenpopulationen und Artendiversität im Feuchtgrünland limitieren, zu untersuchen und herauszufinden, ob unterschiedliche Typen des Managements, die für Niedermoor-Restitution vorgeschlagen werden, geeignet sind, diese Limitationen zu überwinden.

Als die wichtigsten limitierenden Faktoren wurden Diasporenlimitation, Mikrohabitatlimitation und Limitation durch ungünstige Standortverhältnisse berücksichtigt.

Unterschiedliche Managementtypen zur Vergrößerung des Diasporenangebots (Ansaat, Pflanzung und Übertragung diasporenhaltigen Mahdgutes) und zur Veränderung der Standortbedingungen (extensive Beweidung, Mahd, Streuentfernung, Schaffung von kleinflächigen Störstellen, Oberbodenabtrag) wurden untersucht.

DIASPOREN- UND MIKROHABITATLIMITATION

Faktoren, die die Besiedlung eines Standortes durch zwei seltene und regional gefährdete hemiparasitische Feuchtgrünlandarten (*Pedicularis palustris* L. and *Rhinanthus angustifolius* C. C. Gmel.) limitieren, wurden anhand eines faktoriellen Freilandexperimentes untersucht. Diasporen beider Arten wurden in drei verschiedenen Saaddichten (250, 1 250 und 5 000 Diasporen/m²) auf Teilflächen mit unterschiedlichem Störungsgrad (ungestörte Kontrolle, Mahd, kleine und große Störstellen) ausgesät.

Beide Arten stellen sich als diasporenlimitiert heraus: mit steigender Saaddichte erhöhte sich die Anzahl der *Pedicularis*-Keimlinge um das zehnfache (von 37 auf ca. 370 Individuen pro m²), während die Anzahl der *Rhinanthus*-Keimlinge um das 15fache stieg (von 37 auf ca. 560 Individuen pro m²). Zusätzlich kam es mit steigender Saaddichte zu einem erhöhten Etablierungserfolg und zu einer gesteigerten Fruchtproduktion pro Flächeneinheit. Dennoch war die Überlebensrate der Keimlinge im Verhältnis zur anfänglichen Saaddichte beider Arten bei maximaler Saaddichte nur halb so groß wie bei den anderen Saaddichten. Die untersuchten Arten unterschieden sich hinsichtlich ihrer Reaktion auf Störung: Für *Pedicularis* erwies sich das Vorhandensein von Störstellen als notwendige Voraussetzung für eine erfolgreiche Etablierung (sechsfach weniger etablierte Individuen in Teilflächen ohne Störstellen), während fast die gleichen Anzahlen von *Rhinanthus*-Individuen in allen Störungsvarianten inklusive der ungestörten Kontrolle zu finden waren.

Daraus kann geschlossen werden, dass beide untersuchten Arten sich hinsichtlich ihrer Reaktion auf die unterschiedlichen Störungsregime unterscheiden, da Störung die Verfügbarkeit der für sie geeigneten Mikrohabitate in unterschiedlichem Maße beeinflusst. Die großsamigere Art *Rhinanthus* war in der Lage, sich nach Ansatz unabhängig von den unterschiedlichen Störungsvarianten zu etablieren, während *Pedicularis* (eine konkurrenzschwächere Art mit kleineren Samen) auf Störstellen für die Keimung und Etablierung angewiesen und somit mikrohabitatlimitiert war. Zusätzlich waren beiden Arten diasporenlimitiert, da bei höheren Saatedichten größere Anzahlen an Individuen in allen Störungsvarianten auftraten.

EFFEKTE VON STREUENTFERNUNG UND MAHD

Um die Interaktionen zwischen Pflanzenpopulationen limitierenden Faktoren und Standortproduktivität zu untersuchen, wurden die Auswirkungen von Mahd und Streuentfernung auf Keimung, Wachstum und Etablierung zweier typischer Feuchtgrünlandarten (*Silene flos-cuculi* (L.) Clairv. und *Lotus pedunculatus* Cav.) mit Hilfe eines faktoriellen Freilandexperimentes entlang eines Produktivitätsgradienten analysiert. Samen (3 200 per m²) und Jungpflanzen (vier pro 0.0625 m² Teilfläche) beider Arten wurden auf Teilflächen mit unterschiedlichen Kombinationen der Faktoren Streuentfernung (ja/nein) und Mahd (ja/nein) ausgebracht. Das Experiment wurde auf sieben Niedermoorstandorten in Norddeutschland durchgeführt, die sich hinsichtlich der Nährstoffverfügbarkeit, Artenzusammensetzung und oberirdischen Phytomasse voneinander unterschieden.

Für beide Arten wurden positive Effekte von Mahd und Streuentfernung auf die Anzahl der Keimlinge registriert. Des Weiteren unterschied sich die Wirksamkeit von Mahd und Streuentfernung für Keimung und Etablierung entlang des Produktivitätsgradienten: Der Effekt der Streuentfernung war am deutlichsten auf Standorten mit verhältnismäßig niedriger Nährstoffverfügbarkeit und oberirdischer Phytomasse zu beobachten, während sich Mahd hingegen auf hoch produktiven Standorten als wirksamer erwies.

Die Ergebnisse des Experimentes bestätigen die Annahme, dass sich der relative Einfluss einzelner limitierender Faktoren sowie der Effekt unterschiedlicher Managementtypen in Abhängigkeit eines übergeordneten Faktors wie der Standortproduktivität verschieben können.

DIASPORENGEHALT VON MAHDGUT

Die Anwendbarkeit von Mahdgut als Quelle pflanzlicher Diasporen für die Restitution artenarmer Niedermoorstandorte wurde mittels der Analyse von Mahdgut, Aufnahme der Vegetationszusammensetzung und Feststellung der Fruchtreife zum Zeitpunkt der Mahd auf fünf regulär gemähten artenreichen Niedermoorflächen in Norddeutschland untersucht. Der Diasporengehalt im Mahdgut wurde bestimmt und mit der Vegetation verglichen, um zu analysieren, inwiefern der Diasporengehalt des Mahdgutes die Arten in der Vegetation widerspiegelte. Um den Standort mit dem höchsten Gehalt an Diasporen regional seltener und charakteristischer Niedermoorarten im Mahdgut auszuwählen, wurde für alle untersuchten Standorte ein nach Seltenheit gewichteter Niedermoorartenindex berechnet.

Der Anteil der Arten, die sowohl in der Vegetation als auch als Diasporen im Mahdgut repräsentiert waren, lag auf den unterschiedlichen Standorten zwischen 40% und 70%. Eine Cluster-Analyse zeigte die hohe Ähnlichkeit zwischen der Vegetation der Standorte und dem jeweiligen Mahdgut. Dies galt insbesondere für einen der untersuchten Standorte. Die Anzahl der Diasporen reichte von ca. 2 000 bis 12 000 pro m². Die Lebensfähigkeit der Diasporen von Kräutern und Seggen war insgesamt hoch (ca. 80%), während die Lebensfähigkeit der Gräser bei etwa 40% lag. Der Anteil gekeimter Diasporen war für Kräuter, Seggen und Gräser deutlich niedriger (20-50%), was vermutlich durch Samendormanz zu erklären ist.

Anhand des nach Seltenheit gewichteten Niedermoorartenindex der im Mahdgut enthaltenen Diasporen und der Beziehung zwischen Vegetation und Artenzusammensetzung des Mahdgutes wurde ein Standort (eine gering produktive kleinseggendominierte Niedermoorfläche) als Spenderstandort für eine Mahdgutübertragung ausgewählt, auch wenn die Diasporenproduktion pro m² an diesem Standort insgesamt vergleichsweise gering war.

RESTITUTION VON FLUSSTALNIEDERMOOREN

Mahdgut der artenreichen Spenderfläche, die nach dem oben genannten Verfahren ausgewählt worden war, wurde für ein Restitutionsexperiment mit dem Ziel, die Artendiversität auf einer eutrophierten Feuchtgrünlandfläche im Oberen Eidertal zu erhöhen, genutzt. Neben Mahdgutübertragung wurden Effekte von Oberbodenabtrag und extensiver Beweidung auf die Vegetation in einem dreifaktoriellen Freilandexperiment mit vier Replikaten und acht Behandlungskombinationen (auf Teilflächen á 5 x 5 m) untersucht. Das Experiment wurde im Sommer 2001 angelegt, indem entsprechend der jeweiligen Behandlungskombinationen der Oberboden bis zu einer Tiefe von 30 cm abgetragen,

Mahdgut im Verhältnis 1:1 zur Spenderfläche übertragen und Beweidung mittels Auszäunung ausgeschlossen wurde. Zu Beginn des Experimentes wurden Nährstoffe im Boden und Samenbank analysiert, während im Laufe der folgenden vier Jahre (2002-2005) Artenzusammensetzung und Vegetationsentwicklung aufgenommen wurden.

Das Abtragen des Oberbodens hatte einen signifikanten Effekt auf die Abundanz unterschiedlicher Artgruppen: die bereits etablierte Vegetation des Wirtschaftsgrünlandes wurde zurückgedrängt, während Ausläufer bildende Röhrichtarten bei der Wiederbesiedlung der Flächen im Vorteil waren. Die Etablierung seltener und regional gefährdeter Arten nährstoffarmer Niedermoore und Feuchtwiesen aus dem Mahdgut erfolgte mit Ausnahme von *Rhinanthus angustifolius* hauptsächlich auf Teilflächen mit Oberbodenabtrag. Die Auswirkungen extensiver Beweidung waren nach einem Beobachtungszeitraum von vier Jahren von untergeordneter Bedeutung für die Artenzusammensetzung. Allerdings wurde ein Anstieg der Deckung typischer Feuchtwiesenarten verzeichnet.

Die Etablierung von Zielarten nährstoffarmer Niedermoore war dann am erfolgreichsten, wenn sowohl eine ausreichende Anzahl lebensfähiger Diasporen als auch geeigneter Mikrohabitate für Keimung und Etablierung zur Verfügung standen. Größe, Anzahl und Qualität der Mikrohabitate unterschieden sich für jede Art in Abhängigkeit vom jeweiligen Management, des Störungsgrades und der Nährstoffverfügbarkeit der Fläche. In dem Experiment wurde durch Oberbodenabtrag eine maßgebliche Anzahl geeigneter Keimstellen für Zielarten nährstoffarmer Niedermoore und Feuchtwiesen zur Verfügung gestellt, während sich das Mahdgut als hinreichende Quelle für lebensfähige Diasporen erwies. Die Kombination beider einmalig zu Beginn angewandeter Maßnahmen kann zusammen mit einer kontinuierlichen extensiven Nutzung (Beweidung/Mahd) für zukünftige Restitutionsprojekte auf Niedermoorstandorten empfohlen werden.

FOLGERUNGEN

Die vorgelegte Arbeit bestätigt die Vermutung, dass Zielarten der Niedermoorrestitution in vielen Fällen diasporen- und (oder) mikrohabitatlimitiert sind. Somit ist eine Wiederherstellung artenreicher standorttypischer Pflanzengesellschaften in kurzer Zeit nur möglich, wenn diese Limitationen durch die Einführung lebensfähiger Diasporen und Schaffung einer ausreichenden Anzahl geeigneter Keimstellen überwunden werden.

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