

Seedling recruitment in flood-meadow species: The effects of gaps, litter and vegetation matrix

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Abstract

Question: Is the failure of establishment of rare flood-meadow species in habitat restoration primarily due to seed or microsite limitation? How do sown species respond to artificially created gaps and added litter at two neighbouring sites with similar physical conditions but contrasting vegetation matrix (young arable fallow field vs species-poor meadow sward)?

Location: Upper Rhine valley, southwestern Germany, 85 m a.s.l.

Methods: Seeds of six typical flood-meadow species were sown in four treatment combinations of the factors gap creation and litter addition. Seedling recruitment was monitored for three years.

Results: Five of the six species established successfully at both sites largely irrespective of treatments, indicating seed limitation. Only in the small-seeded *Arabis nemorensis*, which was revealed to be strictly gap-dependent at the meadow site, could an obvious microsite limitation be shown. The non-significance of gap treatments in all other species at the relatively high productive meadow site is probably due to biomass removal by mowing in early summer. Only at the extremes of the seed size spectrum did the results meet predictions of plant ecological theory, such as the strict gap dependence of small-seeded species in closed swards or the positive to neutral response of large-seeded species to litter layers.

Conclusions: Species identity was revealed to be the major factor influencing differences in recruitment. Due to the lack of a general trend in the response towards treatments the results support conceptual models that describe the interplay of facilitation and interference as a highly dynamic equilibrium, driven by variable abiotic and biotic marginal conditions.

Keywords: Competition; Grassland; Facilitation; Microsite; Old-field; Restoration; Seed addition.

Nomenclature: Wisskirchen & Haeupler (1998).

Introduction

The availability of seeds (Tilman 1997; Bakker & Berendse 1999; Turnbull et al. 2000) and the lack of suitable microsites for seedling recruitment are increasingly identified as major constraints governing species diversity in temperate semi-natural grasslands (Burke & Grime 1996; Stampfli & Zeiter 1999; Kotorová & Lepš 1999; Zobel et al. 2000; Isselstein et al. 2002).

Recruitment from seeds is a particularly vulnerable stage in the life cycle of plant species and 'regeneration niches' (Grubb 1977) may differ considerably from those of established plants. In comparison with adults, emerging seedlings are usually much more sensitive to both harsh abiotic conditions and competition from neighbouring plants (Grime 2001). Under environmentally benign conditions the inhibitory effects of established vegetation through competition for light, water and nutrients are usually predominant and increase with productivity (e.g. Foster & Gross 1998; Lepš 1999; Suding & Goldberg 1999). In contrast, facilitating effects of established vegetation on seedling recruitment are most often found in unproductive habitats with harsh physical conditions particularly in terms of temperature and moisture supply (Bertness & Callaway 1994; Tielborger & Kadmon 2000).

In temperate semi-natural grasslands the decline in species richness is often caused by the failure of recruitment from seeds, due to enlarged productivity and/or litter accumulation in the course of agricultural intensification or abandonment (e.g. Tilman 1993; Rusch & Fernández-Palacios 1995; Foster & Gross 1998; Lepš 1999). Even in mesic, moderately productive grasslands, gaps created by disturbances of the turf are usually regarded as a prerequisite for successful regeneration by seeds (Bullock et al. 1995; Edwards & Crawley 1999). However, the importance of gap regeneration may differ considerably between species (e.g. Fenner 1978; Kotorová & Lepš 1999; Zobel et al. 2000). Gap dependence is most evident in small-seeded species, which usually exhibit a high light requirement

for germination and a particularly low competitive ability in the seedling stage (Jakobsson & Eriksson 2000; Grime 2001). In contrast, litter accumulation due to cessation of biomass removal by management was often identified as the main factor causing failure of regeneration by seeds and declining species richness in semi-natural grasslands (e.g. Foster & Gross 1998, Špačková et al. 1998; Jensen & Meyer 2001). Again, this seems to apply in particular to relatively small-seeded species (Jensen & Gutkunst 2003), whereas those with larger seeds often show a neutral (e.g. Kotorová & Lepš 1999) or even a positive response (e.g. Gross 1984) to litter cover for various reasons (e.g. protection against desiccation and predation). Generally, gaps can be seen as a localised temporal release from competition (Grime 2001; Suding 2001; Jutila & Grace 2002), whereas litter layers may reinforce interference by established vegetation (Foster & Gross 1998; Grace 2001).

The divergence of findings due to species individuality and marginal conditions makes it difficult to predict the response of species in a particular habitat type without empirical evidence. Seed addition experiments including gap creation and litter removal or addition treatments are particularly helpful for assessing the relative importance of seed limitation and/or the lack of suitable regeneration niches for the failure of recruitment in a particular community (e.g. Hutchings & Booth 1996; Tilman 1997; Zobel et al. 2000; Coulson et al. 2001). Despite their usefulness for testing theory (Eriksson & Ehrlén 1992), such experiments are still surprisingly rare, particularly those that follow the fate of emerging seedlings for more than one season (Turnbull et al. 2000).

Here, this approach was used to identify the reasons for recruitment failure in flood-meadows that have been subject to large-scale restoration measures along the northern Upper Rhine, Germany, during the past 20 years. Despite successful lowering of soil nutrient status and productivity, these efforts have been unsuccessful in re-establishing target species of nature conservation (Donath et al. 2003; Bissels et al. 2004). With focus on the recruitment phase the following questions were posed:

- Is target species enrichment in the studied flood-meadows limited by seed or microsite availability?
- Are there consistent effects of gaps and litter between different species and under contrasting vegetation cover?

Material and Methods

Study site

The study area is situated in the dyke-protected fossil compartment of the Holocene flood-plain of the northern Upper Rhine ca. 30 km southwest of Frankfurt am Main, Germany. The site is located in the depression of a large sediment filled meander that is irregularly inundated by ascending groundwater during high water levels of the Rhine. Soil conditions are characterized by carbon-rich, heavy clays (vertisols) with unfavourable physical features, such as poor aeration and rapid hardening. In conjunction with the relatively dry and warm climate of the region this results in a high variability in soil water potential: While winter and spring often bring floods, summers are very dry, providing adverse conditions for seedling recruitment. During the period of observation, several long-lasting inundations occurred: an exceptionally long flooding event took place directly after sowing from 15.03 - 24.05.2001, causing a considerable delay in the onset of germination. Extended periods of flooding also occurred in spring 2002 and winter 2002/2003.

The study site comprises two adjacent sites with identical physical conditions but contrasting vegetation cover: One site was under intensive arable use until it was abandoned for flood-meadow restoration in autumn 2000. The last crop prior to abandonment was *Phacelia tanacetifolia*, which was cut with a flail mower in October 2000. No further harvesting was undertaken before the seed addition experiment began in early spring 2001.

In the first year after abandonment the vegetation of the arable fallow field was characterized by a sparse cover of annual arable weeds preferring wet site conditions, including *Persicaria lapathifolia*, *Juncus bufonius*, *Sonchus asper*, *Atriplex hastata* and *Veronica catenata*. In the second year these annuals were largely replaced by perennial ruderals such as *Plantago intermedia*, *Cirsium arvense*, *Poa trivialis*, *Polygonum amphibium*, *Juncus articulatus* and *Equisetum palustre* which were still dominant in the third year. After the start of the experiment the vegetation of the arable fallow field was mown once each year in late September, using a flail mower without biomass removal (typical treatment of fallow in the region).

The second site supported a species-poor meadow sward which was created in 1997 on a former arable field by sowing a commercial seed mixture. The sward is dominated by perennial grasses such as *Alopecurus pratensis*, *Phleum pratense*, *Poa trivialis*, *Elymus repens* and the tall weedy herb *Cirsium arvense*. After the onset of the experiment the meadow was cut, and

biomass removed each year at the end of June (traditional hay cutting date in this region), and mown a second time using a flail mower without biomass removal in late September.

Principally, the two vegetation types represent an early and an advanced successional stage in old-field development towards grassland, which is reflected by the predominant plant functional types, i.e. relatively short-lived ruderal herbs vs perennial grasses. The latter are presumed to impose a higher degree of competition on emerging seedlings (e.g. Lepš 1999).

Study species

The studied species, presented in Table 1, are characteristic components of flood-meadows with no, or only limited, potential for clonal spread. This means that they crucially depend on regeneration by seeds to colonize spatially isolated new sites. Apart from *Galium wirtgenii* (common) and *Allium angulosum* (moderately rare) all study species are very rare and severely threatened on a central European scale (Schnittler & Günther 1999). Limited seed dispersal and vulnerability in recruitment from seeds are presumed to be the main reasons for their general rarity, area restriction and the low capacity to colonize new sites (Donath et al. 2003). They also differ considerably in seed mass (Table 1), which is considered to be a major determinant in seedling recruitment (Jakobsson & Eriksson 2000; Grime 2001; Moles & Westoby 2002), particularly in terms of sensitivity to competition from established vegetation (e.g. Kotorová & Lepš 1999).

The seeds for the experiment were collected in bulk in 2000 from natural populations in the wider study region, and stored dry in darkness at room temperature until further use. The potential for germination was tested with two replicates of 400 seeds from each species. Seeds were sown into sterile garden soil under outdoor conditions at the same time as the field experiment started. Seeds were watered regularly during dry periods and germination was followed for two years with seedlings counted and removed once every week.

Experimental design

To test for the effect of gaps and litter on seedling establishment under contrasting vegetation cover, a manipulative experiment with identical design was set up in the young arable fallow field and in the neighbouring meadow sward. Six species were sown in 31.6 cm × 31.6 cm plots (1000 cm²) arranged in four randomized complete blocks. In each block, the following treatments were used:

Table 1. Seed mass (Hölzel & Otte 2004) and germination rate of the study species under optimal outdoor conditions.

Species	Seed mass (mg)	Germination (%)
<i>Allium angulosum</i>	1.74	94
<i>Arabis nemorensis</i>	0.06	87
<i>Cnidium dubium</i>	0.39	8
<i>Galium wirtgenii</i>	0.40	88
<i>Iris spuria</i>	14.62	76
<i>Viola pumila</i>	1.08	66

1. Gap without litter;
2. Gap with litter;
3. Control (no gap, no litter);
4. No gap with litter.

In the gap treatments the plot was stripped and all above-ground vegetation was removed prior to sowing. In the litter treatments the plots were covered with a ca. 2 cm layer of material from a hay bale directly after sowing. The hay bale material originated from a species-poor early mown meadow and did not contain any of the studied species.

On 09.03.2001, 100 seeds of one of the six species (one species per plot) were sown in the central 20 cm × 20 cm part of each of the four treatments per block (24 plots per block). The study species did not occur at the experimental site or, with the exception of *Galium wirtgenii*, in its wider surroundings, making unsown control plots irrelevant.

Seedling establishment was monitored for three years with five counts during the main germination period in 2001 (early June to late September), three counts in 2002 (late May to mid September) and one count in late May 2003.

During the midsummer counts in 2001 and 2002 total plant cover for each plot was estimated visually with an accuracy of 5% and dominant plant species were noted. Additionally, total above-ground biomass was measured with four replicates in mid-June 2002, in both the arable field and the meadow. In the meadow a second cut was performed in mid-August. Dry matter per m² was determined after drying the clippings derived from four randomly placed 1000-cm² quadrats at 60 °C.

Data analysis

The numbers of individuals of each sown species per plot during each count were log ($x+1$) transformed prior to further statistical analyses. To test for differences and interactions between treatments and species over time, a repeated measures ANOVA was performed with species and the treatments gap and litter as fixed factors, block as the random factor and time as the repeated measures

(within subject) factor. Interaction terms with block were used as error terms. Repeated measures ANOVAs were performed separately for the arable fallow field and the meadow site. Differences in plant cover of plots between the gap and litter treatments were checked by a *t*-test for independent samples. Correlations between total vegetation cover and seedling number per plot were analysed by the Spearman rank correlation coefficient. All statistical analyses were carried out with STATISTICA 5.1 (Anon. 1998).

Results

Overall effects of gaps and litter on seedling recruitment

Repeated measures ANOVA revealed a highly significant species, time and species × time effect on seedling recruitment at both sites (Table 3). The latter confirms significant interspecific differences in germination phenology and seedling survival (Fig. 1). Surprisingly, there were no significant treatment effects (i.e. differences in seedling recruitment to the application of gaps and litter) at the arable field site.

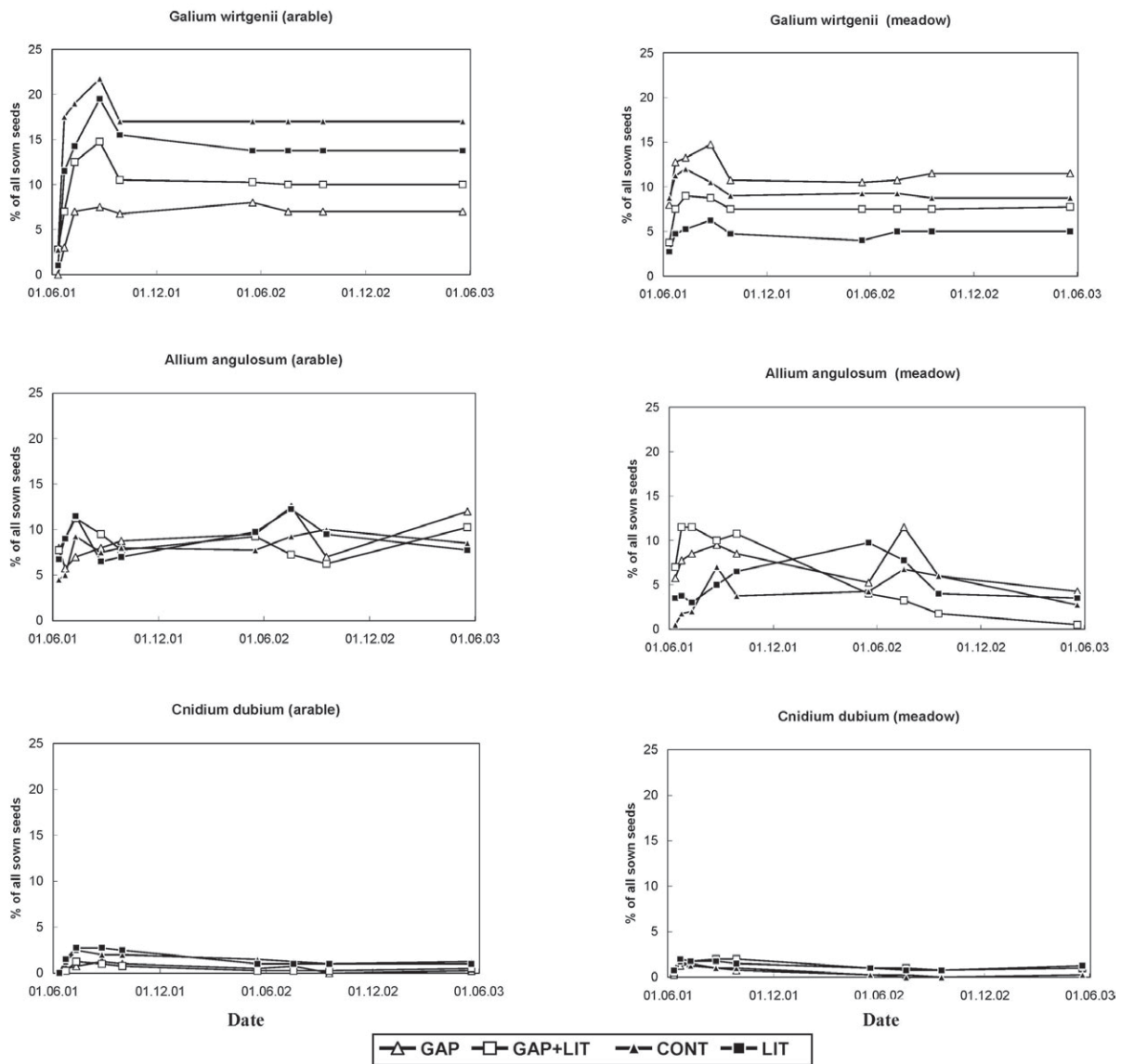


Fig. 1. Effects of treatments on seedling establishment. GAP = plots with artificial gaps; LIT = plots with litter addition; CONTROL = plots without treatment.

Table 2. Vegetation characteristics of the study sites. Different letters in front of the slash indicate significant differences in columns, letters behind the slash those in lines of the same measurement categories. Sites: A = Arable fallow field; M = Meadow (both biomass measurements in mid-June 2002); M₂ = Second growth in the meadow measured mid-August 2002.

Year	Community type /site	Biomass (gm ⁻²)	Cover control (%)	Cover gap (%)
2001	A	-	65.4 ± 16.8 a/a	65.6 ± 22.7 a/a
	M	-	79.0 ± 14.2 b/a	45.4 ± 20.9 b/b
2002	A	134.1 ± 18.3 a	74.0 ± 17.3 a/a	76.0 ± 17.2 a/a
	M	461.6 ± 10.3 b	85.4 ± 6.2 b/a	76.7 ± 18.1 a/b
	M ₂	316.3 ± 79.9 c		

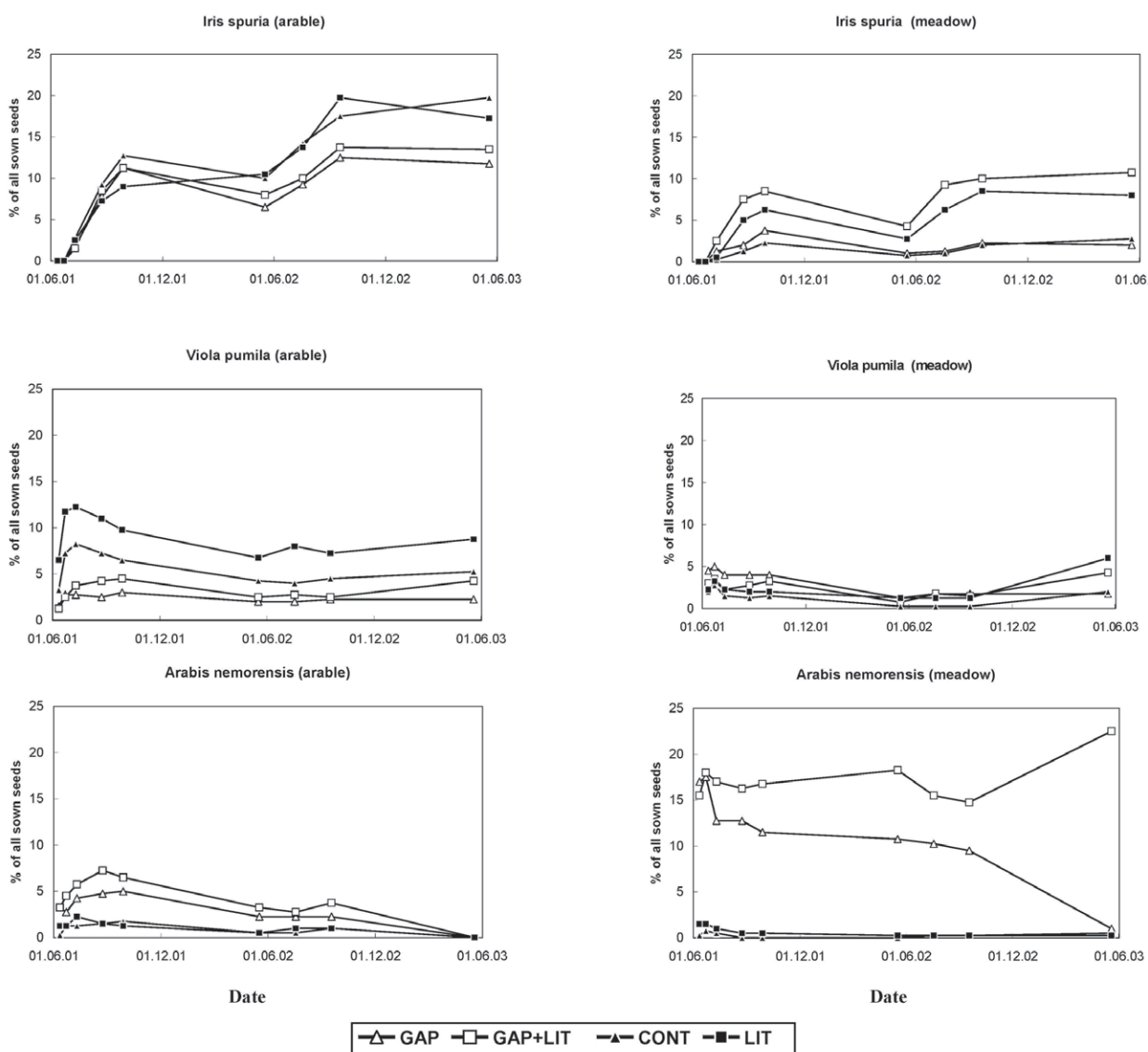


Fig. 1 (cont.)

In contrast, significant gap \times species and litter \times species interactions could be found for the meadow site, indicating that the effects of treatments differed between species. Equally, there was a highly significant gap \times time interaction, confirming that the response towards gaps changed with time. The same was true for litter, the impact of which over time was additionally affected by species identity (litter \times species \times time interaction).

The divergent response towards gaps in the arable field and in the meadow was in line with the measurement of total plant cover (Table 2): within the meadow, gap treatments had significantly lower total plant cover than the control plots during midsummer 2001 and 2002, which means that the gap effect was still measurable in the second year after sod stripping. In contrast, there was no significant 'gap effect' with respect to total plant cover in the young arable fallow field.

Table 3. Results of the repeated measures ANOVA model comparing seedling recruitment of six species (S) in gap (G) and litter (L) treatments at the arable fallow field and the meadow site. Time (T) is the repeated measures factor. Interaction terms with block are used as error terms. Significant effects ($P < 0.05$) are given in bold.

Factor	Effect		Error		F	P
	df	MS	Df	MS		
a. Arable field						
G	1	0.94	3	0.86	1.09	0.3732
L	1	0.45	3	0.75	0.60	0.4964
S	5	11.39	15	0.29	39.93	0.0000
T	8	1.99	24	0.08	24.23	0.0000
G \times L	1	0.09	3	0.19	0.47	0.5408
G \times S	5	2.07	15	1.09	1.91	0.1524
L \times S	5	0.18	15	0.36	0.50	0.7742
G \times T	8	0.06	24	0.06	0.92	0.5207
L \times T	8	0.01	24	0.02	0.48	0.8606
S \times T	40	0.72	120	0.03	21.64	0.0000
G \times L \times S	5	0.24	15	0.27	0.89	0.5116
G \times L \times T	8	0.02	24	0.03	0.63	0.7457
G \times S \times T	40	0.03	120	0.04	0.94	0.5819
L \times S \times T	40	0.02	120	0.03	0.76	0.8415
G \times L \times S \times T	40	0.02	120	0.04	0.45	0.9978
b. Meadow						
G	1	11.86	3	1.92	6.17	0.0890
L	1	0.43	3	0.28	1.51	0.3069
S	5	5.51	15	0.83	6.61	0.0019
T	8	0.29	24	0.12	2.45	0.0429
G \times L	1	0.20	3	1.26	0.16	0.7169
G \times S	5	3.73	15	0.48	7.85	0.0008
L \times S	5	1.40	15	0.29	4.77	0.0083
G \times T	8	0.13	24	0.02	7.32	0.0001
L \times T	8	0.05	24	0.03	1.59	0.1816
S \times T	40	0.33	120	0.06	5.42	0.0000
G \times L \times S	5	0.13	15	0.33	0.39	0.8477
G \times L \times T	8	0.01	24	0.03	0.36	0.9319
G \times S \times T	40	0.05	120	0.05	1.02	0.4535
L \times S \times T	40	0.06	120	0.03	1.92	0.0037
G \times L \times S \times T	40	0.02	120	0.05	0.43	0.9984

The standing crop in mid-June 2002 was more than three times higher in the meadow than in the arable fallow field, whereas differences in total plant cover of undisturbed controls were less pronounced (Table 2).

Response of individual species

There were large differences between species as to total germination rate. While seedling densities were extremely low in *Cnidium dubium* (<2%) they reached up to 20% of all sown seeds in *Iris spuria*, *Galium wirtgenii* and *Arabis nemorensis* (Fig. 1). Generally, maximum seedling counts in the field reached only 15% to 25% of the germination rates obtained in the control experiment on regularly watered sterile garden soil under outdoor conditions (Table 1, Fig. 1).

With the exception of *Allium angulosum* at both sites and *Galium wirtgenii* at the meadow site all species exhibited a significant effect with time (Table 4). Most species reached maximum seedling densities during midsummer of the first season (Fig. 1), followed in some cases by a marked decline towards autumn (e.g. *Galium wirtgenii*). In contrast, the large-seeded *Iris spuria* (Table 1) had a delayed onset of germination starting as late as July and reaching a first peak only in late September (Fig. 1). *Iris spuria* was also the only species exhibiting additional germination in the second year after sowing. After a moderate decline in seedling densities during the first midsummer (drought) and winter (flooding, frost) almost all species showed no further decline in densities during the following years and became successfully established at least as vital vegetative (sub)-adult plants. In *Arabis nemorensis* and *Galium wirtgenii* flowering

Table 4. Results (P as significance of F -values) of repeated measures ANOVA models comparing the effects of gaps and litter on seedling recruitment over three years at the meadow site. For each species a separate repeated measures ANOVA model was calculated in which gap (G) and litter (L) are the fixed factors, block is the random factor (not shown) and time (T) the repeated measures factor. Interaction terms with block were used as error terms. Full species names as Table 1. Significant effects ($P < 0.05$) are given in bold.

Factor	df	<i>Arabis</i>	<i>Cnidium</i>	<i>Galium</i>	<i>Iris</i>	<i>Allium</i>	<i>Viola</i>
G	1	0.012	0.949	0.446	0.876	0.263	0.207
L	1	0.576	0.179	0.006	0.005	0.710	0.201
T	8	0.000	0.005	0.062	0.000	0.352	0.003
G \times L	1	0.801	0.837	0.980	0.804	0.233	0.397
G \times T	8	0.068	0.919	0.535	0.827	0.082	0.517
L \times T	8	0.872	0.764	0.997	0.000	0.018	0.168
G \times L \times T	8	0.823	0.955	0.874	0.931	0.923	0.954

started as early as May 2002, whereas in *Viola pumila* the first seed bearing capsules (cleistogamous flowers) appeared in September 2002 and the first chasmogamous flowers in May 2003. The other three species did not reach a generative state until the end of the observation period. The large decline of the short-lived, mostly biennial, *Arabis nemorensis* in the third year (Fig. 1) was partly due to the harsh environmental conditions (long-lasting flooding followed by severe frost) in winter 2002/2003. The considerable fluctuations in *Allium angulosum* were partly due to herbivory and subsequent resprouting.

The small-seeded *Arabis nemorensis* (Table 1) proved to be completely dependent on gap regeneration at the meadow site (Fig. 1) whereas there was no such effect in the arable field. Accordingly, *Arabis nemorensis* was the only species that showed a highly significant negative correlation (Spearman $r = -0.832$ $P < 0.001$) between recruitment success and total plant cover in 2001.

Galium wirtgenii was the only species which was significantly negatively affected by litter within the meadow (Table 4, Fig. 1). In contrast, litter had a positive impact on recruitment of *Iris spuria* in the meadow site.

Discussion

Seed or microsite limitation

After three years all sown species had established successfully at both sites. Thus, the common failure of re-establishment of these flood-meadow target species in habitat restoration (Donath et al. 2003) is obviously due to seed limitation whereas the lack of regeneration niches seems to be of minor importance. Only in the strongly gap-dependent *Arabis nemorensis* could a significant microsite limitation be confirmed for the meadow. Similar results have been obtained in earlier seed addition experiments (Tilman 1997; Turnbull et al. 2000; Zobel et al. 2000). In accordance with other studies (Kotorová & Lepš 1999; Isselstein et al. 2002) maximum seedling densities under field conditions reached, at best, 25% of potential germination, presumably an effect of seed predation (e.g. Hulme 1994) and/or physical hazards causing early seedling mortality (e.g. Hutchings & Booth 1996).

Final establishment rates as fully developed vegetative or regenerative adults were higher than in other studies, particularly those from dry calcareous grasslands (Kupferschmid et al. 2000; Otus & Zobel 2002). With regard to the low germination rate of seeds in the

control experiment (Table 1), even in the least successful (*Cnidium dubium*) establishment rates were within the range of the other studied species. Remarkably, the best overall recruitment success was found in the most common (*Galium wirtgenii*) and in the rarest and most threatened species (*Iris spuria*). Besides the generally low recruitment in *Cnidium dubium* there was no indication that the rarity of most of the studied species may be predominantly caused by restrictive germination requirements or a shortage in microsites under the prevailing habitat conditions (e.g. Eriksson & Ehrlén 1992). However, we have to take into account that the establishment conditions in the year of sowing were particularly favourable due to improved moisture supply, open sward structure and delayed vegetation development in the course of prolonged spring flooding. In the studied habitat type, which is often moisture limited from early summer onwards, such flooding events proved to have a very positive impact on seedling recruitment (Hölzel & Otte 2003).

Effects of gaps

As predicted by theory (Grime 2001) the species with the smallest seeds (*Arabis nemorensis*) was revealed to be completely gap dependent for successful recruitment in the closed sward of the meadow site. This concurs with results for other rare wet grassland species with small seeds, such as *Gentiana pneumonanthe* (Křenová & Lepš 1996). Surprisingly, none of the other species showed a significant response towards gaps in the meadow site. Several other studies have also reported little difference in recruitment success between gap treatments and 'mown only' plots (Kotorová & Lepš 1999; Jensen & Meyer 2001; Isselstein et al. 2002). Presumably, the inhibiting effect of high plant biomass in the meadow was partly compensated by early mowing in late June, which reduced the amount of standing crop significantly for the rest of the vegetation period (Table 2). Mowing or grazing in productive grasslands can be seen as seasonal competitive release (Huston 1994; Grace 2001; Osem et al. 2002), increasing the amount of light penetration to the soil surface (e.g. Jutila & Grace 2002).

In the arable field site the insignificance of gaps may indicate that seedling recruitment was not hampered by the relative sparse established vegetation. Actually, as early as midsummer of the first season gaps and controls were no longer distinguishable as to plant cover (Table 2). This situation was largely a result of the dominance of annual arable weeds that emerged from the soil seed bank irrespective of gap treatments.

Effects of litter

In the meadow site only in one species (*Galium wirtgenii*) did litter addition have a negative impact on recruitment success. In contrast, the large-seeded *Iris spuria* showed a highly significant positive response towards litter addition. The facilitative effect of litter was probably reinforced by the delayed onset of germination, which is typical of this species due to physical dormancy induced by a particularly thick and compact seed coat (Hölzel & Otte 2004). Litter treatments presumably provided a better protection against desiccation, caused by high temperatures and relatively open vegetation structure prevailing after the first cut of the meadow when germination of *Iris spuria* started. Equally, litter may act as shelter against predation by rodents (Hulme 1994). For large-seeded species neutral or even positive effects of litter on recruitment success have been reported from a number of field studies (e.g. Gross 1984; Kotorová & Lepš 1999). Generally, relatively large-seeded species appear to be less susceptible to litter layers and competition by established plants than species with smaller seeds, which increases the likeliness of successful recruitment in seed addition experiments (Jakobsson & Eriksson 2000; Moles & Westoby 2002).

In the arable field site there was neither a general response towards litter addition, suggesting that positive (protection against desiccation) and negative (shading) impacts probably balanced each other (Holmgren et al. 1997).

Concluding remarks

It can be concluded that even in the closed sward of the meadow site, significant responses to treatments were largely confined to the extremes of the seed size spectrum. At both sites the lack of a more general response towards treatments remains, at least partly, explicable. The obtained results suggest that facilitating or inhibiting effects of neighbouring plants, litter and disturbance regimes on seedling recruitment success are strongly context dependent and it appears to be difficult to define common rules, particularly on the basis of single relatively short-termed surveys (e.g. Tielborger & Kadmon 2000; Turnbull et al. 2000; Kotorová & Lepš 2004). The findings largely concur with the theoretical considerations on the interplay of facilitation and competition in plant communities made by Holmgren et al. (1997). These authors point out the general co-occurrence and dynamical nature of both effects, which are usually in a non-equilibrium state even on a small temporal and spatial

scale. Consequently, variable marginal conditions, in particular less favourable moisture supply during the germination and early establishment phase (e.g. Oomes & Elberse 1976; de Jong & Klinkhamer 1988; Ryser 1993), may rapidly lead to divergent results.

Generally, the findings in this study underpin the great significance of local seed availability and species-specific demands to microsite quality during recruitment for the structuring and maintenance of species diversity in plant communities (Grubb 1977; Eriksson & Ehrlén 1992; Grace 2001).

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