

# Recruitment limitation along disturbance gradients in river floodplains

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## Abstract

**Question:** Along river floodplains lower distribution limits of plant species seem largely determined by their tolerance to rarely occurring floods in the growing season. Such distribution patterns remain fixed for many years suggesting additional effects of winter floods at lower positions. Our objective was to investigate the direct and indirect effects of winter floods on colonization of floodplains in a series of field experiments.

**Location:** River Rhine, The Netherlands.

**Methods:** We measured the direct effects of winter floods on seedling survival and seed removal and survival at low and high floodplain elevation. Indirect effects of winter flooding through changes in the soil were investigated by measuring seedling emergence on soil transplants that were exchanged between high and low floodplain elevation. To investigate indirect effects of floods on the germination environment through changes in the vegetation structure, we measured the effects of vegetation removal on recruitment of sown species.

**Results:** Recruitment was seed limited at both floodplain elevations. An additional effect of vegetation removal on seedling emergence was also observed. Soil types from both zones did not differently affect seedling emergence. Seeds were not removed from the soil surface by a single winter flood. Moreover, seeds remained viable in the soil for at least two years, while the experimental plots were flooded several times during the experimental period. During one of those floods a thick sand layer was deposited at the low zone and subsequently no seedlings were observed anymore.

**Conclusions:** Colonization of low floodplain zones in years between subsequent summer floods is prevented by seed limitation while the direct effects of winter floods are limited except for irregularly occurring sand depositions.

**Keywords:** Flooding; Soil transplants; Sowing experiment.

**Nomenclature:** van der Meijden (1996).

## Introduction

In many wetlands, a clear vegetation zonation can be observed where species' lower distribution limits are determined by the specific tolerance to flooding (Keddy 1984; Sýkora et al. 1988; Silvertown et al. 1999; Voesenek et al. 2004; van Eck et al. 2004). Such distribution patterns are most apparent along elevation gradients with a small variation in water depth and duration, e.g. along lake shores (Keddy 1984) and salt marshes (Huiskes et al. 1995). Similar zonation patterns of plant species can be distinguished along vertical gradients where flooding occurs as a more stochastic event. Such hydrological gradients are typically found in river floodplains where, despite their seasonal component, the timing and duration of natural inundation periods are often unpredictable (Vervuren et al. 2003). Although most floods generally occur during the winter period, vegetation patterns seem largely established by severe but rare flooding events in the growing season (Sýkora et al. 1988; Van Eck et al. 2004, in press). Remarkably, subsequent recolonization of lower floodplain habitats seems virtually absent in years in which summer floods are absent (van Eck et al. 2004). In this paper, we address the relative role of direct and indirect effects of winter floods on the colonization of high-floodplain species at more regularly flooded habitats on the lower floodplains.

Colonization usually starts with the arrival of seeds, which mainly depends on the distance from mother plants and seed dispersal characteristics such as size and morphology (Eriksson & Ehrlén 1992; Nathan & Muller-Landau 2000; Bischoff 2002). After arrival, seeds may be removed again by floods (secondary dispersal) (Schneider & Sharitz 1988; Skoglund & Hytteborn 1990; Nilsson et al. 1991) or decay (Hölzel & Otte 2004) due to low oxygen concentrations in flooded soils (Murdoch & Ellis 1992). If germination does occur, seedlings may also die due to subsequent floods, as seedlings are more sensitive to flooding than adult plants (van der Sman et al. 1993; Voesenek 1990).

Floods may also have indirect effects on species colonization through changes in the soil conditions that

are unsuitable for regeneration. Prolonged floods may potentially lead to differentiated soil particle sorting (Olff et al. 1997; Abernethy & Willby 1999) which affects the soil water holding capacity. Consequently, seedling emergence and growth may be different at low- and high-elevation sites (Keddy & Ellis 1985; Lenssen et al. 1998). Furthermore, despite the fact that floods potentially thin the vegetation and reduce competitive interactions, the remaining vegetation may still inhibit subsequent colonization.

In a series of field experiments we examined: (1) the degree of seed limitation at low and high floodplain elevation; (2) whether winter floods may act as a secondary dispersal agent for seeds; (3) the persistence of seeds in the soil at low and high elevation floodplain zones; (4) the effect of vegetation structure and soil type on seedling emergence and seedling survivorship at low and high floodplain elevations.

## Material and Methods

### *Species and study area*

All experiments were performed at the 'Ewijkse Plaat' (51°53' N 5°45' E), a sandy floodplain site along the River Waal, the main branch of the River Rhine in The Netherlands. For most experiments two elevations were compared. In the low zone ( $11.52 \pm 0.12$  m + NAP (Dutch Ordnance level)) a mixed *Agrostis stolonifera*, *Elytrigia repens* and *Rumex crispus* grassland occurred, while the higher zone ( $14.21 \pm 0.04$  m) is dominated by *Festuca rubra*, *Plantago lanceolata*, *Achillea millefolium* and *Eryngium campestre*. The lower zone is mostly flooded for long periods during winter and early spring (October - April) while floods from May - September are rare. During winter the high elevation grassland is only occasionally flooded for very short periods. The most recent extreme summer flood at 13 m occurred in 1987.

The selected species are all typical of the high-elevation sites. They are hemicryptophytes (Raunkjær 1934) and flower and disperse seeds between early May and November. Seeds were collected between 1999 and 2001 from single populations along the River Waal and stored at room temperature under dry and dark conditions. Fresh and stored seeds are not dormant.

During the experiments, the lower zone of the research site was flooded several times, whereas the high elevation zone was flooded only twice, all during the winter period (Fig. 1 in App. 1). During the fourth, very deep flood in 2002, sand was deposited in the low floodplain zone and covered all plots with a thick layer:  $10.1 \text{ cm} \pm 1.4 \text{ cm}$  (seed addition experiment) and  $7.9 \text{ cm} \pm 1.4 \text{ cm}$  (soil type experiment), respectively ( $n = 5$ ).

### *Indirect effects of flooding: vegetation structure*

To examine the effects of seed and recruitment limitation, we measured seedling recruitment as a function of elevation, seed addition and vegetation removal in a full factorial randomized block design. At both the high and low elevations, ten blocks were laid out in a line parallel to the river, and distance between blocks in a line was at least 2 m. Within each block, ten plots were established in a square grid at 30 cm distance. Each plot was delimited with a PVC ring with a diameter of 15 cm and a height of 2 cm, which was gently pushed into the soil to soil surface level (plot surface =  $0.07 \text{ m}^2$ ).

For each species, plots were randomly assigned to the following treatments: '+ seed addition - vegetation' and '+ seed addition + vegetation'. The sowing experiment was carried out with *Plantago lanceolata*, *Daucus carota*, *Achillea millefolium* and *Rumex thyrsiflorus*, with only one species sown per plot (100 seeds per plot). Only one control plot '- seed addition - vegetation' and one plot '- seed addition + vegetation' were established in each block for all four species to determine natural seedling emergence. Hence each block contained one replicate per treatment combination.

A pre-sowing germination test in which seeds were put on two layers of moistened filter paper (Schleicher & Schuell, Dassel Germany) in petri dishes and put in a germination room with  $16 \text{ hour } 25 \mu\text{mol.m}^{-2}.\text{s}^{-1}$  PPFR (Philips TL33) at  $25^\circ\text{C}$  and 8 h darkness at  $10^\circ\text{C}$ , showed that the potential germination capacity for the selected species ranged from 75 - 99% (average of five replicates of 100 seeds per species). Seeds were sown after the peak of natural seed dissemination: *R. thyrsiflorus* and *P. lanceolata* were sown on 13.09.2001 and *A. millefolium* and *D. carota* on 03.10.2001. For open plots, all above-ground vegetation was clipped once at the substrate surface just before the seeds were added. From October 2001 until September 2002 all plots were monitored every four or six weeks except during the main flooding period of the lower zone. During monitoring the total number of germinated seeds per plot was recorded. Because emerged seedlings were not removed, only the net number of seedlings was recorded which was the result of germination and seedling mortality. During the experimental period, the lower zone was flooded six times and the higher zone twice, all during winter (Fig. 1 in App. 1).

### *Indirect effects of flooding: soil type*

To determine whether soil type at different elevations might explain species distribution, we transplanted soil cores within and across the low and high zone and measured recruitment of sown *Plantago lanceolata*.

Before the start of the experiment we observed high seedling densities of this species at high floodplain elevations. Therefore *P. lanceolata* was considered to be a sensitive phytometer species for detecting effects of soil type.

The following soil core transplantations were carried out: high to low elevation, low to high elevation, high to high elevation (control) and low to low elevation (control). Soil transplantation was performed, using PVC tubes (diameter 15 cm; surface 0.07 m<sup>2</sup>), which were pushed into the soil to a depth of 25 cm. The PVC tube with a soil core was taken out of the soil and moved into a hole with the same diameter and depth at the other or a similar zone. Soil was transplanted by gently pushing the core out of the tube into the hole, without disturbing the texture of the soil. Plots were delimited with PVC rings as described above. Ten replicate plots per treatment (elevation × origin soil combination) were established in ten blocks (per block: one original soil core and one soil core originating from the other zone) in a full factorial design at high and low elevation zones parallel to the river. On 13.09.2001, vegetation in all plots was clipped at the surface and subsequently 100 seeds of *P. lanceolata* were added to each plot. Spatial arrangement of blocks and plots and counting procedure were similar to the experiment described above.

#### *Direct effects of flooding: seed viability in the soil*

To determine the effect of burial time and floodplain elevation on seed viability, seeds were buried for different periods of time in two floodplain zones: 50 seeds of each of the species *Plantago lanceolata*, *Thalictrum minus*, *Galium mollugo*, *Medicago falcata* and *Daucus carota*, were placed in separate nylon bags (5 × 5 cm, 0.8 mm mesh size). One seed bag for all five species each were put together in a larger nylon bag (16 × 11 cm, 0.8 mm mesh size), and were buried on 19.12.2000 at a depth of 5 cm at both elevations in five blocks. The distance between blocks was 5 m and within each block we randomly assigned each larger bag to a duration of 6, 12, 18 or 24 months and subsequently buried each bag separately keeping a minimum distance of 30 cm between each bag. A pre-burial germination test (conditions the same as mentioned earlier) was performed to obtain an estimate of the potential germination capacity (five replicates of 50 seeds per species). Seeds of *M. falcata* were gently scoured with fine sandpaper to break dormancy but pre-treatment of other species was not considered necessary. After removal from the soil, viability of the seeds was tested by germination trials under the same conditions as mentioned earlier. The seeds were monitored for germination once a week. If a radicle appeared the seed was considered as germinated

and removed from the petri dish. All seeds that failed to germinate turned out to be decayed. Those rotten seeds were easily pulverized by rubbing them between fingers. Monitoring was continued for a maximum of 6 weeks.

#### *Direct effects of flooding: seed removal experiment*

For six species we examined whether winter floods may act as a secondary seed dispersal agent. The selected species were: *Plantago lanceolata*, *Daucus carota*, *Medicago falcata*, *Galium mollugo*, *Thalictrum minus* and *Anthriscus sylvestris*. Seeds of the species differ in size and morphology. Seed size ranged from ca. 1 mm in *G. mollugo* to ca. 7 mm in *A. sylvestris*. Most seeds have a smooth or ridged seed (or fruit) coat and do not possess specific dispersal appendages, except fruits of *D. carota* which are equipped with small hooks (adaptation to zoochory).

We selected three elevations that were expected to differ in flood duration in winter. The low and high zones are at the same floodplain levels as in the experiments described above, i.e. 11.52 and 14.22 m, while the mid-level was in between those zones at 12.87 m. On 08.11.2000, plastic pots (diameter 12.5 cm, height 10 cm) were buried up to the soil surface and filled with a soil core originating from the same location without disturbing the soil texture. In each zone 12 pots were buried along two parallel lines perpendicular to the river (six pots per line). Distance between pots within and between lines was 20 cm. To each pot 100 seeds per species were added (in total 600 seeds per pot) and gently pushed into the soil surface.

In January 2001 the low and middle zone were flooded for 8 and 6 days respectively, whereas the highest zone was not flooded during this period (Fig. 1 in App. 1). Just before the onset of the flood, six randomly chosen control pots per zone were covered with fine meshed nylon cloth (mesh diameter = 0.8 mm) to prevent potential seed removal by the flood. Immediately after withdrawal of the flood at 15.01.2001 all pots were carefully collected and stored at a temperature of 5 °C in the dark to prevent seed germination. Subsequently the total soil content of each pot was gently rinsed with tap water above a sieve (mesh diameter 0.5 mm) and the numbers of seeds per species were counted. Seeds of the different species were easy to recognize visually.

#### *Statistical analyses*

Data with regard to seed removal and seed viability were analysed using two-way ANOVA (STATISTICA 5.5, StatSoft Inc.). Effect of seed addition, vegetation removal, soil type, floodplain elevation and census date

on seedling emergence were analysed using repeated measures analysis of variance (SAS statistical package, SAS Institute Inc.). In these analyses we considered block as a random factor nested within elevation. As a consequence we used block as an error term for elevation, all other terms were tested against residual. Prior to all ANOVA's we tested homogeneity of variances and normal distribution of residuals.

**Table 1.** Summary of repeated measures ANOVA of effects of vegetation (with and without), floodplain elevation (low and high), and census date on seedling emergence and establishment (ln-transformed data) for each of four species (*P. lanceolata* (Pl), *R. thyrsoflorus* (Rt), *D. carota* (Dc) and *A. millefolium* (Am)). During the first season (2001) only seed addition plots were analysed. For the second season (2002) we analyzed the effects of vegetation structure (with and without vegetation), seed addition (with and without) and census date on seedling emergence and establishment only for plots at high floodplain elevation. We used repeated measures analyses of variance to study both variation between subject (main effects) and variation within subject (repeated factor Time). *F*-values and significance levels (\* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p < 0.001$ ) are presented as well as MS values for residuals. For 2002 results, significance levels of the within subject effects are corrected by using the Greenhouse-Geiser (G-G) correction factor  $\epsilon$ . df = degree of freedom.

Source of variation	df	Pl	Am	Rt	Dc
<b>2001</b>					
Between					
Elevation	1	2.23	1.70	4.27	0.67
Block(Elev.)	18	0.86	0.76	0.59	0.87
Vegetation	1	54.58 ***	193.37 ***	1.31	24.25 ***
E × V	1	0.17	1.06	0.41	2.50
Residual (MS)	18	0.68	0.77	3.82	1.51
Within					
Time	1	6.76 *	4.18	147.44 ***	22.04 ***
T × Elevation	1	7.51 *	1.78	0.15	0.91
T × Block(Elev.)	18	1.65	0.61	2.99 *	2.92 *
T × Vegetation	1	0.48	0.30	0.25	7.39 *
T × E × V	1	3.84	0.49	0.89	3.57
Residual(T) (MS)	18	0.17	0.07	0.17	0.30
<b>2002</b>					
Between					
Block	9	0.89	0.95	3.63 **	0.45
Seed	1	71.34 ***	134.49 ***	62.03 ***	10.17 ***
Vegetation	1	0.40	10.20 **	7.51 *	0.01
S × V	1	2.53	10.20 **	9.77 **	0.01
Residual (MS)	27	1.54	1.44	0.85	0.43
Within					
Time	4	12.00 ***	17.78 ***	19.85 ***	34.59 ***
T × Block	36	1.63	1.10	1.44	0.72
T × Seed	4	7.17 ***	17.78 ***	3.81 *	34.59 ***
T × Vegetation	4	1.09	0.90	0.92	3.54 *
T × S × V	4	1.36	0.90	0.94	3.54 *
Residual(T) (MS)	108	0.21	0.09	0.22	0.09

## Results

### Indirect effects of flooding: vegetation structure

In the first autumn (2001) seedlings of all four species emerged at both zones and in both vegetation treatments in the seed addition plots (Fig. 1). Seedlings were present during the following winter. In the plots without seed addition only *P. lanceolata* and *A. millefolium* seedlings emerged, and did so in relatively low numbers. Hence, all species appeared to be seed-limited with no clear difference in degree of seed limitation between elevations.

Due to the low seedling emergence in plots without seed addition we only included seed addition plots in subsequent analyses of first season data. Results indicated that in 2001 vegetation removal significantly increased seedling emergence in *P. lanceolata*, *A. millefolium* and *D. carota*, but there was no significant interaction with elevation (Table 1). Only germination of *R. thyrsoflorus* was not affected by vegetation removal.

After the sand coverage due to winter floods, emerged and new seedlings were no longer observed at the low zone. Before the sand coverage seedlings were qualitatively observed in lower-elevation plots, also after the first two floods. Due to the deposition accident, only data from higher elevation plots were analysed for the 2002 season. Also in 2002 species turned out to be seed limited at high floodplain elevation (Fig. 1 and Table 1). No seedlings of *D. carota* and *R. thyrsoflorus* emerged in plots without seed addition. Along the higher zone, a gradual decline in seedling densities occurred for all species in the seed addition plots (Fig. 1). Only in *A. millefolium* and *R. thyrsoflorus* the effect of seed addition on seedling emergence was also dependent on the vegetation structure with more germination in treatments in which vegetation was removed (significant interaction of Seed × Vegetation in Table 1).

### Indirect effects of flooding: soil type

Seedling emergence of *P. lanceolata* during the first season (2001) did not significantly differ between soil types (original soil or transplanted soil) regardless of the elevation where the soil core was transplanted to (Fig. 2 and Table 1 in App. 1). Also for the second season (2002) the results revealed no significantly different effect of substrate on seedling emergence and recruitment along the higher floodplain zone (Table 1 in App. 1). In 2002 in the low zone sand deposition prevented the emergence of a second cohort of seedlings whereas first year seedlings were no longer observed (Fig. 2).

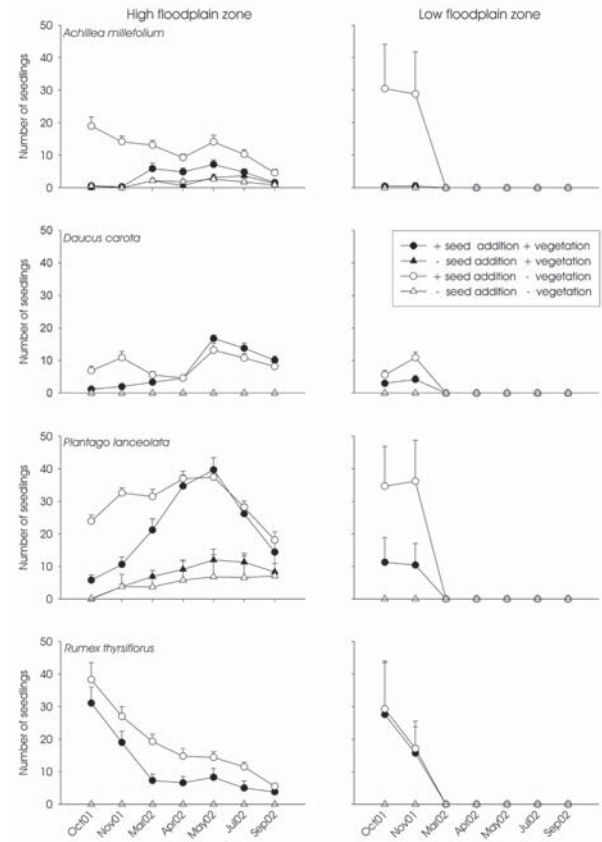


### Direct effects of flooding: seed viability in the soil

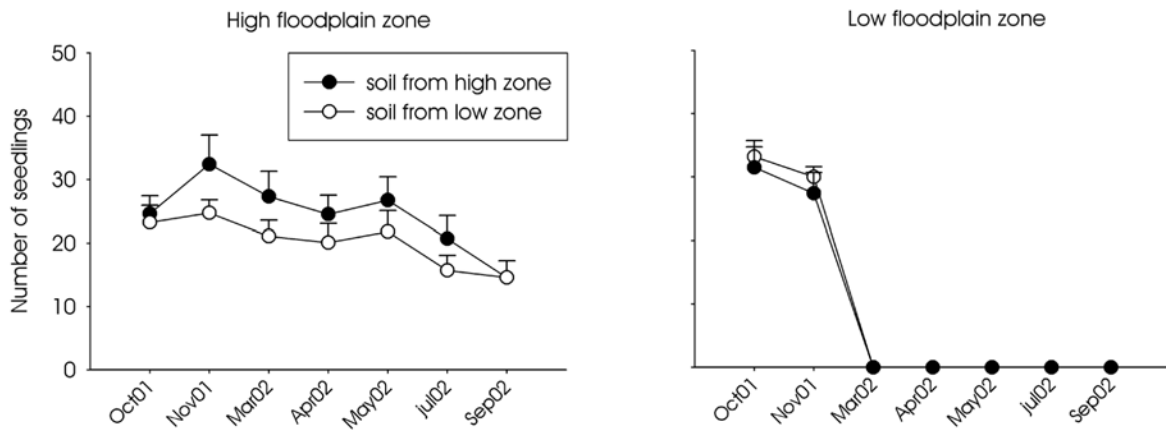
During the study period, both zones were flooded several times during winter (Fig. 1 in App. 1). Pre-burial germination ranged from 55 to 96% (Fig. 3). For the majority of species, the percentage of seeds that germinated, decreased only slightly with burial duration regardless of the floodplain zone where seeds were buried (Fig. 3 and Table 2 in App. 1). Differences between floodplain elevations did therefore not affect seed viability during a 2-year period. Germination of *T. minus* seeds did not even change compared to the pre-burial germination percentage after 2 years of burial. In *M. falcata* and *P. lanceolata* an effect of elevation on seed viability was observed, but seeds at low elevation were even more viable than those at high elevation (Table 2 in App. 1).

### Direct effects of flooding: seed removal

At the experimental site only the low and mid-level zones were flooded during the research period (Fig. 1 in App. 1). For all species relatively high seed numbers were recovered in the plots along the three zones (Fig. 4). Surprisingly the smallest number of seeds was retrieved in the upper non-flooded zone for all species (Fig. 4). In *A. sylvestris* and *D. carota* a significant interaction existed between floodplain elevation and coverage of the plots (significant  $E \times C$  interaction in Table 2), indicating larger removal of seeds in the covered plots, but only at high elevation. This may have been the result of predation by earth worms which were able to access covered plots by holes in the bottom of the pots. Moreover, after sampling of the plots germinated seeds were observed in covered plots at the most upper zone which may be due to higher temperatures under the cloth coverage.



**Fig. 1.** Number of emerged seedlings (result of germination and death) of *Achillea millefolium*, *Daucus carota*, *Plantago lanceolata* and *Rumex thyrsiflorus* during 2001 and 2002 in plots (0.07 m<sup>2</sup>) in response to seed addition (with and without seed addition) and vegetation structure (with and without vegetation) at low and high floodplain elevation  $\pm$  SE ( $n = 10$  plots per species per zone per treatment).



**Fig. 2.** Number of emerged seedlings (result of germination and death) of *Plantago lanceolata* during 2001 and 2002 in response to substrate type (original soil or transplanted soil) in seed addition plots (0.07 m<sup>2</sup>) without vegetation at low and high floodplain elevation  $\pm$  SE ( $n = 10$  plots per zone per treatment).

**Table 2.** Results of analysis of variance for number of seeds in plots after a flood under influence of floodplain elevation (low, mid and high) and coverage (covered and uncovered plots) for *Medicago falcata* (Mf), *Plantago lanceolata* (Pl), *Thalictrum minus* (Tm), *Galium mollugo* (Gm), *Anthriscus sylvestris* (As) and *Daucus carota* (Dc) (STATISTICA 5.5, StatSoft, Inc.). F values and significance levels are presented (\* =  $p < 0.05$ ; \*\* =  $p < 0.01$  and \*\*\* =  $p < 0.001$ ) as well as values for residuals (MS). df = degree of freedom. Number of replicates = 6.

Effect	df	F-values					
		Mf	Pl	Tm	Gm	As	Dc
Elevation	2	10.06 ***	6.47 **	10.29 ***	15.32 ***	9.96 ***	20.68 ***
Coverage	1	0.09	1.04	2.02	0.21	0.14	4.40 *
E × C	2	0.99	0.29	2.31	2.15	5.27 *	5.13 *
Residual (MS)	30	219.93	329.54	338.59	262.22	232.11	186.9

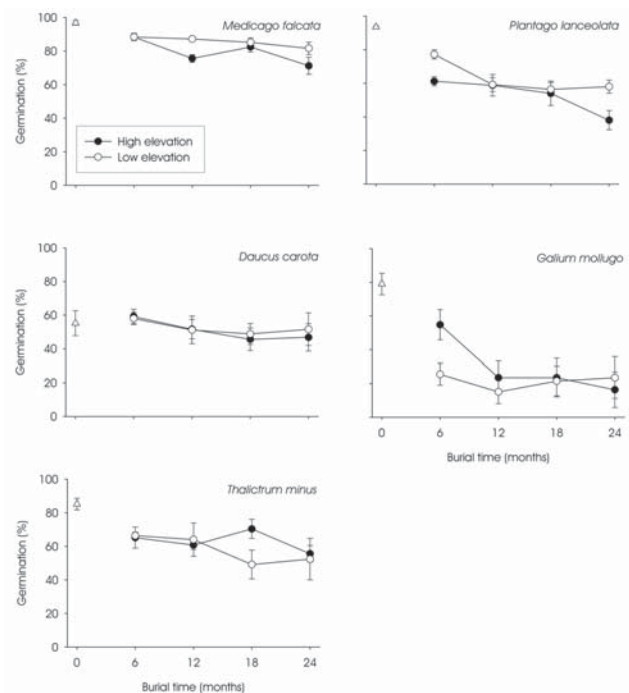
## Discussion

In this study we examined the different processes responsible to plant establishment at lower floodplain zones. Our results suggest that seed availability is an important determinant of colonization of low floodplain zones in years without summer floods, rather than removal of seeds by winter floods or reduced viability at low elevations. Direct effects of winter floods on colonization seem limited except for radical but erratically occurring sand depositions.

The last severe summer flood in our study area occurred more than 13 years before the data for our study were collected in which flood sensitive species were established to higher elevations (Sýkora et al. 1988; Vervuren et al. 2003; van Eck et al. 2004). Together with the lack of appropriate dispersal appendages in the majority of species, the distance between source populations at high elevation and the sites at low elevation (ca. 40 m) seems the major reason for the lack of recruitment, in spite of the 13 years time to bridge this distance. Due to sand deposition at the lower elevation plots, we have not been able to compare the degree of seed limitation at both elevations, as most natural germination occurred in the second year. However, our results do suggest that also at high elevation, seed limitation limits establishment of species at the local scale. Although at low elevations the vegetation structure is relatively open, the effects of vegetation removal at low and high elevated sites were of similar magnitude, suggesting that winter floods do not significantly facilitate seedling emergence by opening the vegetation structure. Lenssen et al. (2004) have recently shown that competitive intensities are not altered either under flooding.

Several studies have recognized the role of water flow for seed dispersal and consequently for structuring plant communities along river floodplains (Schneider & Sharitz 1988; Nilsson et al. 1991; Huiskes et al. 1995). Johansson & Nilsson (1993) reported for a river in

northern Sweden that flooding relocated seeds among sites. Huiskes et al. (1995) demonstrated that seeds in salt marshes could be dispersed over long distances by tidal water movement. Others found only minor changes in the propagule bank before and after floods (Cellot et al. 1998). We found no direct effect of winter floods on the removal of seeds from the soil surface. Hence, the observed seed limitation in low floodplain zones does not seem to be the result of secondary dispersal of seeds by floods. Apparently the seeds were efficiently incorporated into the soil or attached to the soil surface preceding the flooding event. In addition, seed buoy-



**Fig. 3.** Percentage of germinated seeds of *Medicago falcata*, *Daucus carota*, *Thalictrum minus*, *Plantago lanceolata* and *Galium mollugo* after 6, 12, 18 and 24 months of burial at low and high floodplain elevation ( $\pm$  SE). Triangles indicate the pre-burial germination percentages ( $\pm$  SE).  $n = 5$ .

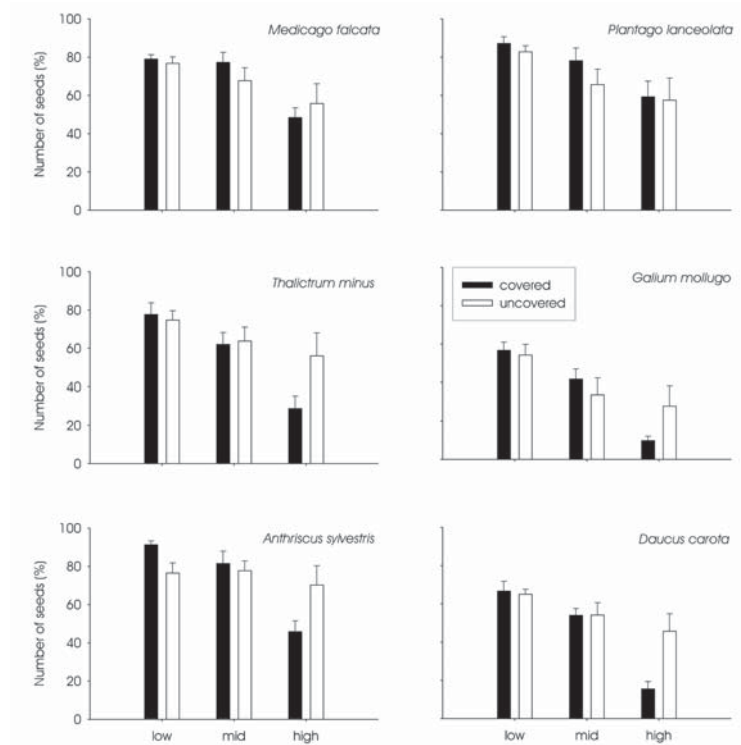
ancy may be lost after seeds have been lying on the ground for several weeks (Nilsson et al. 1991). However, stronger stream power may possibly lead to larger seed removal. Remarkably, the lowest seed numbers in this experiment were recovered in the upper most zone. Hence, in our study sites, the conditions at high elevations seem even less suitable for seed viability on the ground. This may be due to a higher biogenic activity (e.g. earth worms) in zones that are less frequently disturbed by floods.

In contrast to other studies (Lenssen et al. 1998; Keddy & Ellis 1985), we found no differential seed survival and seedling emergence along the flooding gradient prior to winter flooding. Instead, seeds in the lower, regularly flooded zone remained viable for at least two years. In *M. falcata* and *P. lanceolata*, seed viability was even higher at lower positions. Seedling emergence was not reduced at lower elevations and since we did not find any difference either in *P. lanceolata* emergence between original soil and soil transplants it may be concluded that neither elevation nor soil type decreases seedling emergence at lower positions prior to winter flooding.

The only direct effect of winter flood that we observed was sand coverage preventing seedling emergence and killing all existing seedlings at the lowest elevation after a very deep winter flood. The frequency extent of sand deposition will depend on geomorphologic

characteristics of the floodplain and the temporal variation in discharge, sediment load and velocity of the river water (Olf et al. 1997; Abernethy & Willby 1999; Vervuren et al. 2003). Therefore the frequency of sand deposition occurrence is unpredictable and will differ between years and sites, and seedling emergence and establishment success will vary concomitantly.

In summary, our study highlights two major reasons why colonization of lower elevation floodplain habitats by species from higher elevations is limited between severe flooding events in the growing season. Firstly, recruitment is prevented by the limited availability of seeds. Interestingly, dispersal limitation not only occurs in fragmented (meta) populations (Ehrlén & Eriksson 2000; Primack & Miao 1992; Ouborg 1993; Bischoff 2002) but also along unfragmented disturbance gradients. Two explanations can be given for the colonization limitation. 1. The normal seed rain apparently cannot bridge the relatively short distance between the source population and sink sites, even over many years. But if seeds arrive at lower floodplain elevations they are able to germinate. 2. Seedling emergence and survival are locally prevented due to abiotic stress caused by direct effects of winter floods. The magnitude and frequency of this effect in river floodplains is hard to quantify. Once these hurdles have been taken, adult plant survival seems less negatively affected by detrimental effects of winter floods than summer floods as shown by van Eck



**Fig. 4.** Percentage of seeds in covered (nylon gauze) (closed bars) and uncovered (open bars) pots after a winter flood across three floodplain zones (low, mid and high elevation) for *Medicago falcata*, *Plantago lanceolata*, *Thalictrum minus*, *Galium mollugo*, *Anthriscus sylvestris* and *Daucus carota*. Bars represent untransformed means  $\pm$  SE ( $n = 6$  plots per species per zone per treatment).

et al. (2004, in press).

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