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Experiments and observations on seed dispersal by running water in an Alpine floodplain

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Summary

1 In-stream dispersal and floating capacity of 18 pioneer plants (nine chamaephytes, eight hemicryptophytes and one shrub) from alluvial floodplains on the upper Isar (Bavaria, Germany) were studied using field and laboratory experiments between 1994 and 1996.
2 Drift collection of seeds with nets at the water surface proved unsuitable because of the great amount of invertebrates drifting along the river, though it allowed an estimation of the amount of drifting seeds. In August and September we found over 9,000 drifting seeds per meter stream width and day or over 120,000 seeds over the whole stream width in 24 h. Sediment-filled baskets proved to be better traps but were often destroyed during flooding periods. Although drift collection was of limited value for sampling seeds in a highly dynamic floodplain, water transport of viable seeds could be demonstrated for nine of the 18 species.
3 In laboratory experiments, in which seeds were placed into a beaker, stirred up to five days and then used for germination tests, seeds of 16 of the 18 species showed a moderate to good floating capacity. Only two species had seeds that could not float longer than a few minutes (*Gypsophila repens* and *Silene vulgaris* ssp. *glareosa*).
4 We hypothesised that dispersability decreases with increasing seed mass, but the assumption that heavy seeds are not dispersed over great distances is valid only for environments without the possibility of in-stream dispersal.

Keywords: alluvial floodplains, River Isar, pioneer plants, floating capacity, in-stream dispersal

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Introduction

Early in the 20th century, alluvial floodplains with an extensive and diverse system of channels and gravel bars were a regular feature of alpine landscapes also extending into the foothills of the Alps. Some specialised plant communities characterised these habitats. At present, remnants of alluvial floodplains in the European Alps are restricted to the upper reaches of mountain streams (Martinet & Dubost 1992; Müller 1995). At these sites flood-induced turnover of gravel bars is still high, and the bars are nutrient-poor and often very dry habitats (Müller 1995).

Plant species colonizing gravel bars have to be stress-tolerant with respect to drought, flooding and sedimentation (Müller 1995; Bill *et al.* 1997); they also have to be able to colonize suitable habitats fast and in sufficient numbers. Under natural conditions we expect an equilibrium between the loss and re-establishment of local populations, at least within larger sections of a floodplain. Since numerous sites and stands may be destroyed by a single flood, it is advantageous for riparian pioneer plants to be widely dispersed. A mosaic of patches with pioneer vegetation allows for rapid recolonization of new sites because the distance to a potential source of colonizers is short. In the context of an obvious need for efficient dispersal in a variable environment (Venable & Brown 1988; Bakker *et al.* 1996), the question of how seeds of pioneer plants on gravel bars are dispersed is of particular interest.

Water-engineering structures, such as weirs and reservoirs, may obstruct dispersal by running water. This must have consequences for conservation management, if seeds of the mostly endangered species are dispersed by water in great amounts and depend on this kind of dispersal (Johansson *et al.* 1996).

There are several means of riverine seed transport: drifting on the surface, floating in the water and moving along the bottom of the stream or with the sediment. If movements of seeds were linked to sediment transport, then seed banks would be an integral part of new sediment deposits (cf. Bonn & Poschlod 1998). However, such seed banks were not observed in the floodplain studied (Bill 1999), although they are a common feature of many lowland rivers which have finer sediments (e.g. Poschlod 1996). Therefore, drift appears to be the most likely mechanism for seed dispersal by water. Drift would allow seed deposition to co-occur with the deposition of fine sediment. Presence of fine sediment in turn favours germination of seeds, because fine sediment can hold water for a sufficient length of time.

The following questions were addressed in this study:

(1) To what extent are seeds of the pioneer species of alpine floodplains able to be dispersed by water?
(2) Are special morphological adaptations necessary for efficient water transport?
(3) Does dispersability decrease with increasing seed mass?

The experiments reported here are part of a larger research project on the ecology and conservation of braided river sections in the Alps (Plachter & Reich 1998).

Study area

The study area is located in the Bavarian Alps at the northern edge of the Karwendel mountain range near the border between Germany and Austria (700–950 m a.s.l.). The area, along the upper Isar between Mittenwald and Lenggries (Fig. 1), is part of the last fairly natural alluvial floodplain remaining in Germany. The stretch between Vorderriß and the Sylvenstein reservoir in particular has retained high fluvial and sediment dynamics, mainly because of one tributary, the Rißbach. In spite of the diversion of water for hydroelectric purposes, the stretch upstream from Vorderriß also retains large patches of habitat for pioneer species (Reich & Erber 1999). At the weir at Krün large quantities of water are diverted at medium flow, while peak floods and sediment transport are not greatly reduced. Downstream from this weir normal discharge is restricted to 4.8 $m^3 s^{-1}$ in summer and 3.0 $m^3 s^{-1}$ in winter. This causes a constant flow without much variation for most of the year. Upstream from Krün there are no weirs, so water discharge, amount of sediment transported and flood regime remain unaltered. Because of the rather narrow valley there is no broad floodplain in this stretch. The pioneer plant communities have nearly vanished from downstream sections which are severely impacted by the Sylvenstein reservoir and other flood control measures (Reich 1994). The study area holds the last sizeable population of *Myricaria germanica* in Germany (Bill *et al.* 1997).

Methods

Our research in the alluvial floodplain of the Isar was carried out between 1994 and 1996. A set of species characteristic for alluvial floodplains in the European Alps was selected. The species include 17 perennial plants (nine chamaephytes, eight hemicryptophytes) and one shrub (cf. Table 4; nomenclature according to Oberdorfer 1990).

Two methods were applied to assess surface drift in the river. In 1994 we started drift collections with nets. Because this method proved to be inadequate, we continued in 1995 and 1996 with drift collections using sediment baskets. These methods allowed us to assess qualitatively whether there were seeds drifting in the river. To quantify seed transport and to estimate transport distances different techniques are necessary.

The transport of seeds during flood events could not be investigated directly, as the methods used did not endure the immense forces created by high water. We were also not able to collect driftline material (cf. Nilsson & Grelsson 1990; Skoglund 1990; Bonn & Poschlod 1998), as drift material was deposited all over the floodplain and thus no distinct line was formed. Instead, we used floating experiments in the laboratory to assess the potential of different seeds for instream dispersal.

DRIFT COLLECTIONS WITH NETS

From April to October 1994 five drift-nets (mesh size 400 μm) were placed in the main channel of the upper Isar at river km 247.6 (Fig. 1) during average flow level (4.8 $m^3 s^{-1}$). Stream width at the sampling site was 13 m, with no parallel channel. Nets (opening width 25 cm) were anchored with steel bars, so that the water surface could be sampled to a depth of 5 cm (Hering & Plachter 1997). Once each month the drift nets were exposed for 24 h. However, due to the extremely high numbers of invertebrates in the drift (7.3 to 18.2 million over the whole stream width a day), collections had to be limited to 5 min each hour during a 24 h period. Therefore one sample represents a total of 120 min. For practical reasons, the samples obtained had to be reduced to subsamples of *c.* 6% of the total volume. Seeds were sorted from the subsamples and determined using a reference collection. Due to the subsampling, the results had to be multiplied by a factor of 160 to obtain estimates for the total number of seeds transported per meter stream width in 24 h at the water surface.

No germination experiments could be done with the seed material, as all the material had to be stored in alcohol immediately after collection to preserve the invertebrates for a related study (Hering & Plachter 1997).

Mean current velocity at the water surface was determined by measuring the time it took an orange to travel 100 m (ten replicates, cf. Hynes 1970). Measuring current velocity allowed for the estimation of the total drift per volume of water.

DRIFT COLLECTIONS WITH SEDIMENT BASKETS

Pre-trials were carried out in 1994 using small plastic baskets (length x width x height = 30 x 20 x 15 cm^3). The baskets were filled with sand and gravel. Previous studies had shown that this sediment contained no seeds (Bill 1999). The baskets were covered with mesh wire and a board to prevent aerial input and exposed in the Isar. We found that 3–4 weeks of exposure were sufficient to trap a large number of seeds, while most animals managed to escape. As baskets were protected from aerial inputs, transport via the stream was the only possible mechanism for seeds to get into the baskets.

Starting in May 1995, sediment baskets were exposed at four sites in the main channel of the Isar: just above the town of Mittenwald (river km 262.2), between Krün and Vorderriß (river km 240), at Vorderriß (river km 232.2) and below the Sylvenstein reservoir (river km 223.8; cf. Fig. 1); 2 x 6 baskets were exposed at each of the sites. Baskets were attached to iron bars so that they could still be moved up and down and thus their height could be adjusted to changing water levels (Fig. 2). Basket height was readjusted weekly

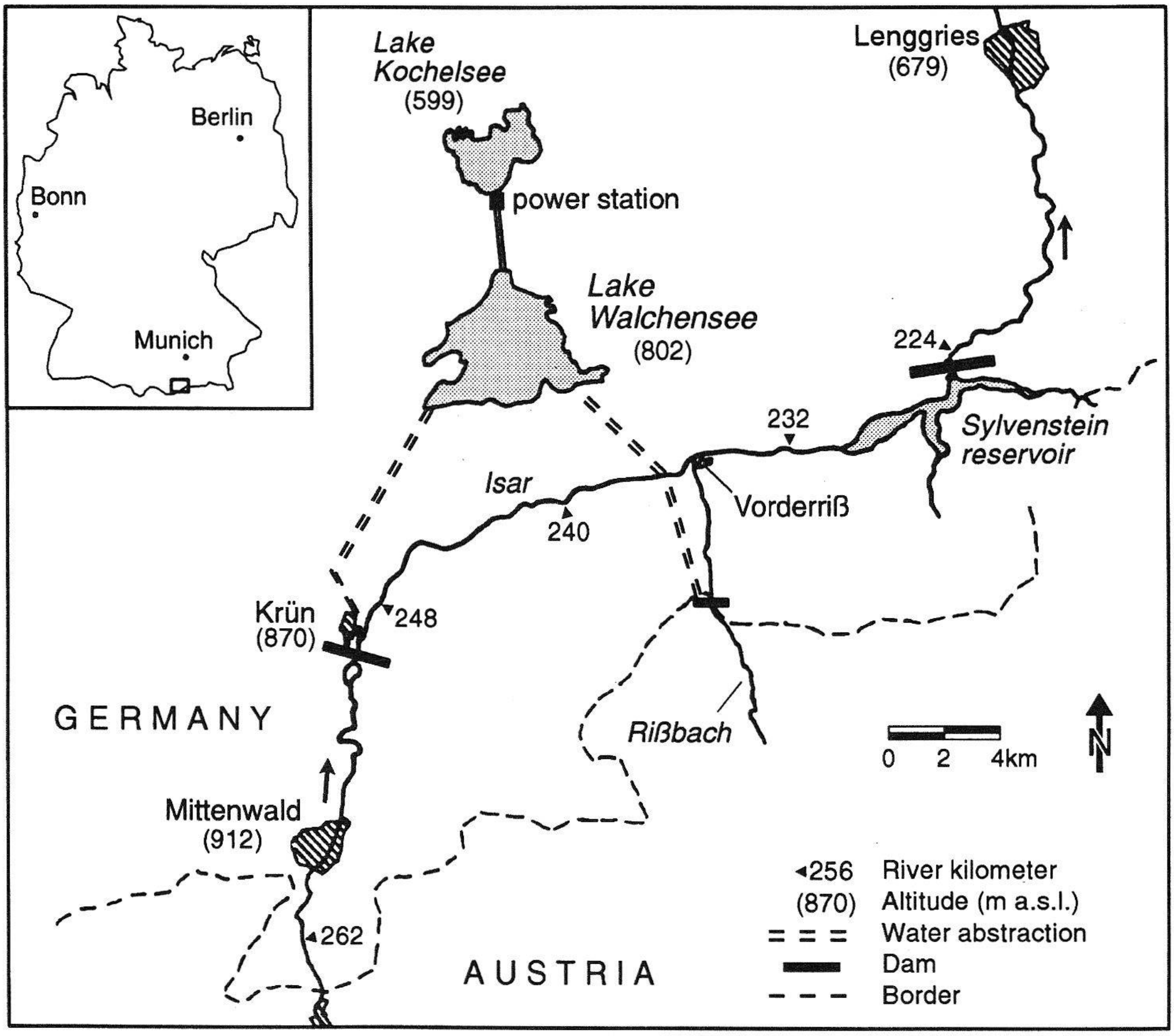

Fig. 1. The study area along the upper Isar (Bavaria, Germany) with the most important weirs, dams, reservoirs and diversion channels between Mittenwald and Lenggries. Inset: Location of the study area within Germany.

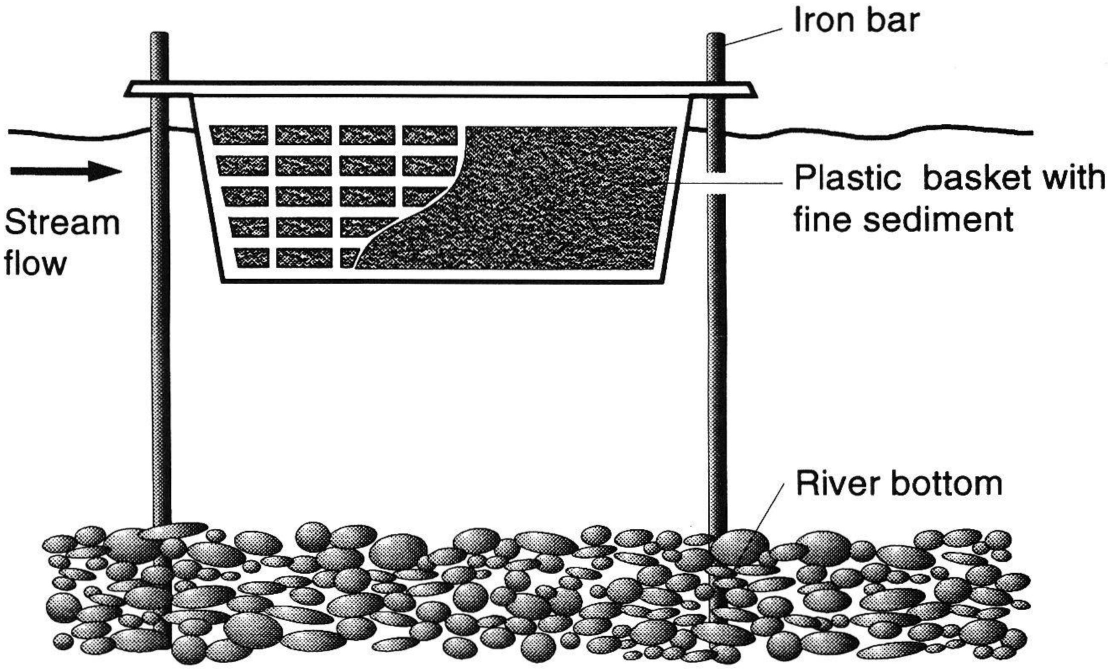

Fig. 2. Sediment baskets used for drift collections (shown without mesh wire and board).

to maintain the depth of exposure (10 cm, sampling of the surface drift). Baskets were exposed for one month, they were then recovered and the contents transferred to germination trays covered with a sterile horticultural substrate. The germination trays were located on the river banks close to the sites of basket exposure. All germination trays were covered with a screen (mesh size 0.2 mm) to prevent input of seeds. The trays were inspected for seedlings once or twice every two weeks. Seedlings were counted, and removed after determination. The germination experiments were terminated in October. Several floods during 1995 caused the loss of sediment baskets and germination trays which were therefore replaced. During high floods no sampling was possible.

The experiments were continued in 1996 using six sediment baskets at Mittenwald and 32 baskets at the Vorderriß site. All baskets and germination trays were lost due to a flood in June. The experiments were then continued, using 2 x 6 baskets in Vorderriß. However, a second flood in June again destroyed the sampling devices and the trays. Consequently, experiments were restricted to the Mittenwald site and finally terminated in August 1996.

No results were obtained from baskets exposed below the Sylvenstein reservoir, as the overflow volume and thus water levels in the stream fluctuated considerably even over short time periods. Therefore, surface drift could not be collected continuously.

IN-STREAM FLOATING EXPERIMENTS

Floating experiments were conducted in the upper Isar during August and September 1996 during normal flow. Freshly collected seeds were used in these experiments. There was almost no wind during the experiments. Between 3,000 and 5,000 seeds of *Dryas octopetala, Erigeron acris* ssp. *angulosus* and *Tolpis staticifolia* were released into the main channel at Vorderriß (river km 235.6). Marking of seeds was not possible, as this would certainly have altered floating abilities as pre-

Table 1. Estimated number of seeds in the 1994 drift-net collections, calculated as number of seeds per meter stream width and hour. The calculation is based on 24 x 5 min netting per month with 5 x 25 cm^2 net width

Species	*n*	Seeds per meter stream width and hour						
		Apr	May	Jun	Jul	Aug	Sep	Oct
Agrostis gigantea	8				13	40		
Alnus incana	13		13		27	13	13	20
Betula pendula	91		20	7	40	147	373	20
Calamagrostis pseudophragmites	25					167		
Pinus mugo	2			7	7			
Salix-fruit stand	2		7	7				
Undetermined	8				13	40		
Sum	149	0	40	21	100	407	386	40

trials showed. To "re-capture" seeds, four drift nets were exposed in the Isar for 70 min at a point 1 km downstream from the site of seed release (methods as above, stream width 10 m, no other channels). All apparently viable seeds (*sensu* Roberts 1981) were sorted from the samples and determined. Mean current velocity at the water surface during the floating experiment was also measured (method as above).

To calculate the whole stream transport, recapture totals had to be multiplied by 10, as only about 1/10 of the total stream width was sampled.

LABORATORY FLOATING EXPERIMENTS

Floating abilities of different plant species have been investigated by several authors by putting the seeds in water-filled containers and counting every day the number of sunken seeds (Guppy 1906; Praeger 1913; Romell 1954; Parker & Leck 1985; Poschlod *et al.* 1996; Danvind & Nilsson 1997). In this study a modified technique was applied: 25 seeds of each of the 18 species were placed into a beaker and stirred (*c.* 100 rounds min^{-1}); there were (4–)6 replicates. To simulate flood conditions half of the replicates were run with sand and fine gravel added to the beakers. Floating seeds were counted after 1, 2, 6, 12, 24 h and thereafter daily. When more than 95% of the seeds had sunk to the bottom of the beaker or after 5 days at the latest, the seeds were recovered and tested for germinability. Germination tests were run on moist filter paper in a growth cabinet (14L:10D, 22 °C during the day, 14 °C during the night; Poschlod *et al.* 1996). Germination (i.e. appearance of the radicule) was checked after 1, 2, 4, 7, 10, 14, 21 etc. days. For comparison, germination rate and time were also assessed for seeds which had been stored dry at room temperature. Twelve species were chosen to repeat the floating and subsequent germination experiments with seeds that had been stored for six months at room temperature.

The average seed mass was determined for three samples of 50 or 100 freshly collected, air-dried seeds from each species. We obtained data on the specific weight from Müller-Schneider (1986).

Results

DRIFT COLLECTIONS WITH NETS

The drift nets collected 149 seeds from only six species (Table 1), 61% were of *Betula*

***Table 2.** Drift collections with sediment baskets in 1995 and 1996, given as number of seedlings in the germination beds*

	Number of seedlings in the germination beds									
	1995						1996			Total
	May	Jun	Jul	Aug	Sep	Oct	Jun	Jul	Aug	
Number of baskets	18	12	42	21	18	18	6	6	6	147
Salix eleagnos / S. purpurea	62	2								64
Agrostis gigantea	11	1	6	8	1		1	8		36
Poa alpina	6		2	10	2			2		22
Petasites paradoxus	12	1								13
Poa annua				2		3	1			6
Tolpis staticifolia	1			5						6
Leontodon hispidus ssp. *hastilis*				3			2			5
Calamagrostis pseudophragmites				4						4
Dryas octopetala					3					3
Hutchinsia alpina				1			2			3
Arabis alpina	1				1					2
Barbarea vulgaris				1	1					2
Carduus defloratus	1									1
Juncus sp.	1									1
Undetermined	18	6	9	8	1					42
Sum	113	10	17	42	9	3	6	10	0	210
= Seedlings per basket	6.3	0.8	0.4	2.0	0.5	0.2	1.0	1.7	0.0	1.4

pendula. In August and September the calculated amount of drifting seeds was over 9,000 seeds per meter stream width and day, or over 120,000 seeds over the whole stream width in 24 h.

Mean current velocity was 75 m min^{-1} (= 4.5 km h^{-1}). Thus, drift nets sampled about 562 m^3 of water during the 24 x 5 min collection intervals. The maximum number of seeds transported near the water surface, therefore, is estimated to be 1.8 seeds m^{-3} during base flow (August).

DRIFT COLLECTIONS WITH SEDIMENT BASKETS

In the sediment baskets 14 species were found which are characteristic for gravel bars of alluvial floodplains (Table 2). Overall, 210 seeds, mainly *Salix eleagnos* and *S. purpurea,* emerged from the germination trays. The largest number of seeds in the sediment baskets was collected in May 1995. However, this was mainly a result of a large number of willow seedlings sprouting from just a few fruits.

Seedling emergence was also high in August, when grass seeds (*Agrostis gigantea, Calamagrostis pseudophragmites* and *Poa alpina*) dominated the collections. In May and August, besides the species listed in Table 2, some additional species which are rather untypical for gravel banks were encountered at Mittenwald and a few at sites between Krün and Vorderriß, but not at the sample site further downstream. These eight species occur more often on fine riverine sediments or in wet meadows: *Cardamine amara* (4 seedlings), *Deschampsia cespitosa* (2), *Elymus cani-*

Table 3. Number of seeds collected in four drift nets after upstream release

Date	23.8.96	26.8.96	25.9.96
Released			
Dryas octopetala	2000	2000	
Erigeron acris ssp. *angulosus*		3000	4000
Tolpis staticifolia	1000		
Re-captured (max.)			
Dryas octopetala	0,2%	1,1%	
Erigeron acris ssp. *angulosus*		0,4%	0,2%
Tolpis staticifolia	0,3%		
Additionally captured			
Agrostis gigantea	1	2	5
Arabis alpina	1		
Betula pendula	6	6	5
Calamagrostis pseudophragmites	25	18	8
Carex flacca	1	3	4
Carex flava	2	4	
Leontodon hispidus ssp. *hastilis*			1
Pinus mugo		1	1

nus (2), *Myosotis palustris* (1), *Taraxacum officinalis* (1), *Urtica dioica* (4), *Veronica anagallis-aquatica* (2) and *Veronica beccabunga* (5).

IN-STREAM FLOATING EXPERIMENTS

During the in-stream floating experiments, seeds from all the species used in the experiments were recaptured (Table 3). Recapture rate was relatively low: a maximum of 2–11% of the seeds released were transported over a 1 km stretch to the sample site (surface transport) within 70 min of the release.

Mean current velocity during the experiments was 75 m min^{-1} (= 4.5 km h^{-1}) and as the air was calm during the experiments, most seeds collected probably originated from the sample released into the river further upstream. However, the difference in recapture rates of *Dryas* seeds released on August 8th and on August 26th reveals the degree of scatter which might have affected the results of the experiments.

LABORATORY FLOATING EXPERIMENTS

Floating time for most seeds was >1 h for 16 of the 18 species studied. However, for twelve species floating time was reduced when sediment was added (Table 4); only for *Hutchinsia alpina* floating time increased when sediment was added. For six species higher floating times were recorded for seeds which had previously been stored; storage never caused a decrease in floating time. The species studied in the experiments could be classified according to their floating abilities (Table 4, Fig. 3).

The first group contains two species with rather heavy seeds (*Gypsophila repens, Silene vulgaris* ssp. *glareosa, c.* 0.7–1 mg) which have previously been characterised as "boleochore", i.e. shed from capsule and dispersed by wind (Müller-Schneider 1986). These species were not represented in the drift collections (Tables 1–3).

Group 2 is composed almost exclusively of species which have previously been charac-

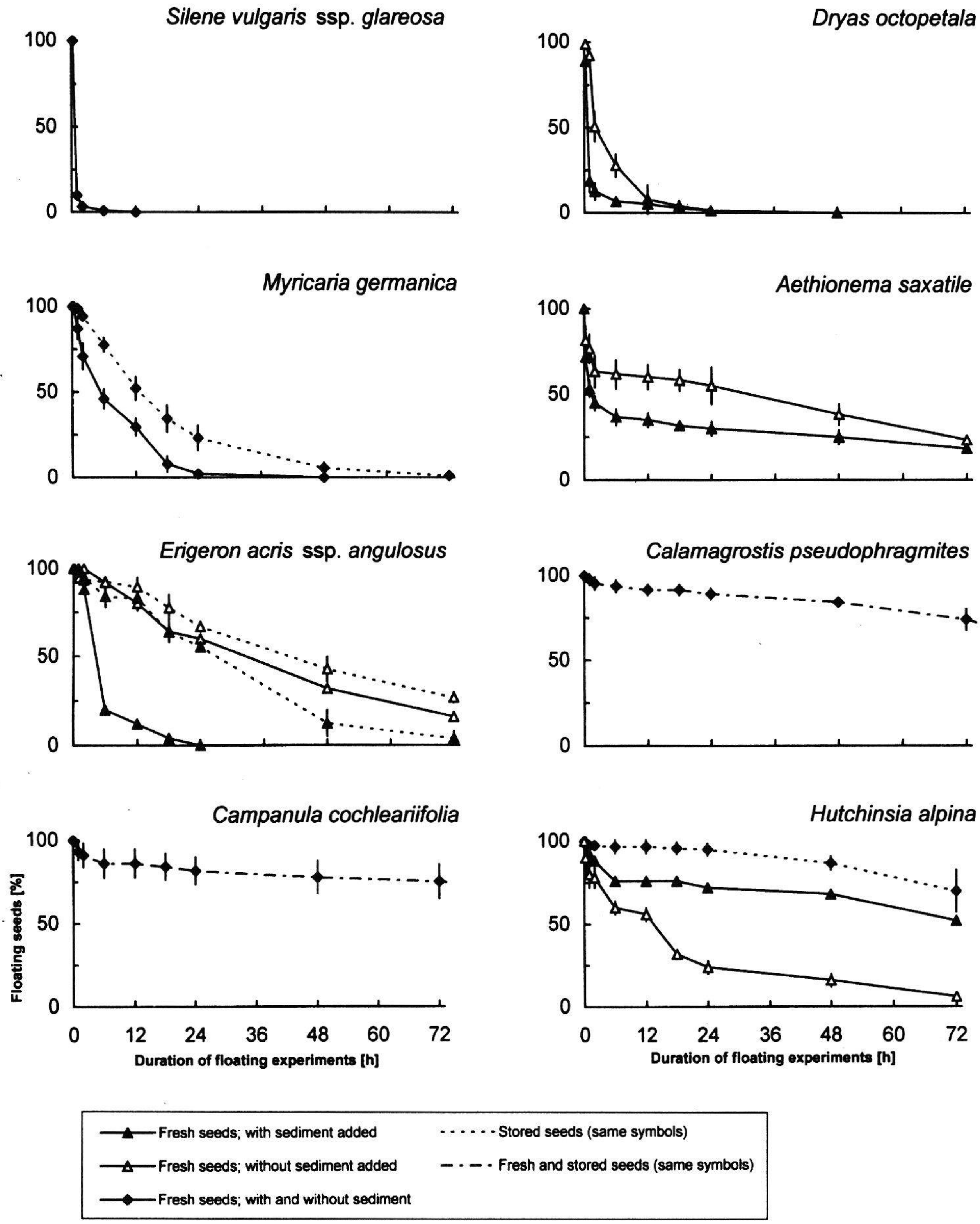

Fig. 3. *Floating capability of eight seed species. Given is the mean percent of seeds still floating (2–3 trials with 25 seeds each). Bars, SD (>3 replicates). Type 1, seeds do not float ($f_{50} = 0, f_{max} < 6$ h); type 2, seeds float badly ($f_{50} <$ 6 h, $f_{max} < 2$ d); type 3, few seeds float well ($f_{50} <$ 1–2 d, $f_{05} >$ 3–4 d, $f_{max} < 5$ d); type 4, many seeds float well ($f_{50} >$ 2–3 d, $f_{05} > 5$ d, $f_{max} > 5$ d) (cf. Table 4).*

Table 4. *Seed floating capabilities (laboratory experiment). Abbreviations: w/o, with/without sediment added; f_{50}/f_{05}, time after which 50/5% seeds still float; f_{max}, time after which all seeds are sunk; floating capability after storage, stored for six months (except* Myricaria *stored one week); g_{50}, time for 50% seeds to germinate; means of dispersal, according to Grime* et al. *(1988): windp, seeds plumed; windc, shed from capsule; windw, seeds winged/flattened*

Species	Storage	Sed.	Floating time (h)			Germination		Seed mass (mg)	Means of dispersal
			f_{50}	f_{05}	f_{max}	rate (%)	g_{50} (d)		
Type 1									
Gypsophila repens	Fresh/dry	w/o	0	0	0	65	7–10	0.67	windc
Silene vulgaris ssp. *glareosa*	Fresh	w/o	0	1	1	45	10	1.02	windc
Type 2									
Dryas octopetala	Fresh	w	1	12	24	45	4–7	0.84	windp
		o	2	18	24	45	4–7		
Erigeron acris ssp. *angulosus*	Fresh	w	6	18	18	80	4	0.09	windp
		o	48	96	96	70			
Leontodon hispidus ssp. *hastilis*	Fresh/dry	w	6	24	48	60	7	0.95	windp
	Fresh/dry	o	6	48	48	60	7		
Myricaria germanica	Fresh	w/o	6	24	48	66	2	0.07	windp
	1 week	w/o	12	48	60	38	2		
Petasites paradoxus	Fresh	w	6	18	48	40	2	0.57	windp
		o	24	72	96	40	2		
Saxifraga caesia	Fresh	w/o	1	12	24	60	42	0.03	windc
Tolpis staticifolia	Fresh/dry	w	2	18	24	60	7–10	0.30	windp
	Fresh/dry	o	6	24	72	60	7–10		
Type 3									
Aethionema saxatile	Fresh	w	2	>96	>120	30	7–14	0.38	windw
		o	24	120	>120	30	7–14		
Arabis alpina	Fresh	w	6	24	60	30	14–21	0.19	windc
		o	18	>96	>120	30	14–21		
Arabis pumila	Fresh	w	12	48	60	5	4–7	0.22	windc
		o	24	>96	>120	5	4–7		
Erigeron acris ssp. *angulosus*	6 month	w	24	72	72	50	4	0.09	windp
		o	48	120	>120	50	4		
Hieracium piloselloides	Fresh	w	18	72	120	70	7–10	0.10	windp
	6 month	w	48	96	120	45	7–10		
	Fresh/dry	o	48	120	>120	45	7–10		
Hutchinsia alpina	Fresh	o	18	72	96	60	7–10	0.31	windc
Kernera saxatile	Fresh	w/o	48	120	>120	25	10–14	0.12	windc
Type 4									
Agrostis gigantea	Fresh	w	72	>120	>120	90	2–4	0.07	windw
		o	>120	>120	>120	90	2–4		
Arabis alpina	6 month	w	96	>120	>120	35	4–7	0.19	windc
		o	>120	>120	>120	35	4–7		
Arabis pumila	6 month	w/o	>120	>120	>120	7	4–7	0.22	windc
Calamagrostis pseudophragmites	Fresh/dry	w/o	120	>120	>120	25	4	0.06	windp
Campanula cochleariifolia	Fresh/dry	w	120	>120	>120	4	14	0.04	windc
	Fresh/dry	o	>120	>120	>120	4	14		
Hutchinsia alpina	Fresh	w	72	120	>120	60	7–10	0.31	windc
	6 month	w/o	96	>120	>120	75	7–10		
Kernera saxatile	6 month	w/o	72	>120	>120	90	4–7	0.12	windc
Saxifraga caesia	6 month	w	48	48	>120	85	28	0.03	windc
		o	72	>120	>120	85	28		

terised as "trichometeorochore", i.e. seeds plumed and dispersed by wind. The seed mass of these species are between 0.03 and 0.95 mg. *Dryas octopetala, Leontodon hispidus, Petasites paradoxus* and *Tolpis staticifolia* seeds were found in the drift collections. However, no seeds were obtained from *Myricaria germanica* and *Saxifraga caesia.*

The third group comprises species with seed mass of 0.1–0.3 mg, e.g. *Aethionema saxatile, Erigeron acris* ssp. *angulosus* and *Hieracium piloselloides.* Floating time of seeds of these species increased after dry storage at room temperature; most species were boleochorous. Only *Arabis alpina* and *Hutchinsia alpina* seeds were found in the drift collections.

Finally, group 4 comprises mainly long-floating, mostly boleochorous species; mean seed mass within this group were about 0.1 mg. However, *Arabis pumila, Campanula cochleariifolia* or *Saxifraga caesia* seeds were not recorded in the drift collections.

Discussion

CRITICAL COMMENTS ON THE METHODS

Drift collection of seeds with nets or sediment baskets proved to be of limited use in the highly dynamic alluvial floodplain of the upper Isar (cf. Staniforth & Cavers 1976). However, considering frequency and intensity of flood events at the study site it is unlikely that any other method would have been more effective to collect floating seeds. It appears that drift collections are better suited to investigate seed dispersal along less dynamic stretches of streams (e.g. Poschlod 1996). Along the upper Isar a visible driftline was not available for collecting seeds. The lack of such driftline material may not be a general property of alluvial streams, since Poschlod *et al.* (1997) recorded high numbers of viable seeds in the driftline material along the upper Loire (France) after a major flood. However, only a small portion of the recorded seeds belonged to pioneer plants of gravel bars.

The drift collections with sediment baskets yielded qualitative results with respect to transport in the current and subsequent germination.

As information gained from the field surveys was incomplete, results from floating experiments in the laboratory were of additional importance. Our experimental approach attempted to simulate mixed seed and sediment transport in a riverine environment by stirring the seeds in a beaker. Addition of fine sediment probably decreased surface tension and thus yielded results which may come close to the actual field conditions during a flood. Experiments without stirring tend to overestimate floating abilities of seeds. Thus, studies measuring floating time in a beaker (Guppy 1906; Praeger 1913, Romell 1954; Parker & Leck 1985) reveal maximum floating ability which may be correlated with maximum seed dispersal distances.

The increase in floating abilities after storage under dry conditions is probably due to drought or shell hardening and thus increased water-repellency of the seed or fruit coat (cf. Howe & Smallwood 1982; Bewley & Black 1994). Storage times of six months appear unlikely in the field, as seeds tend to germinate as soon as conditions are favourable, though there might be some storage during winter. Seed mass alone is insufficient to determine floating abilities. Rather, specific weight (Müller-Schneider 1986) and above all water repellency, morphology and shape of the seeds are important (Howe & Smallwood 1982). However, most theoretical studies concerned with seed dispersal use absolute weight (or size) as the key parameter.

The stochasticity of key events is a general problem for research in highly dynamic ecosystems. Key events such as peak floods may be most important for dispersal and colonization, in spite (or because) of their rare occurrence (Plachter 1996). Processes like peak floods are hard to study directly and probably even harder to simulate (Silvertown & Lovett Doust 1993).

THE SIGNIFICANCE OF WATER-LINKED DISPERSAL

The significance of transport by running water for long-distance dispersal has frequently been emphasized (Ryvarden 1971; Salisbury 1975; Murray 1986; Nilsson & Grelsson 1990; Johansson & Nilsson 1993; Bakker *et al.* 1996; Danvind & Nilsson 1997). Studies on seed dispersal in water were either concerned with aquatic plants (e.g. Cook 1987), salt marshes and ocean beaches (Murray 1986; Huiskes *et al.* 1995), lake shores, or the colonisation of islands (e.g. Rydin & Borgegard 1991) or medium and lower sections of river catchments (Lhotska & Kopecky 1966; Kelley & Bruns 1975; Nilsson & Grelsson 1990; Poschlod *et al.* 1997). Little research has been done on upper reaches of rivers and streams (but see Ryvarden 1971; Stöcklin & Bäumler 1996; Danvind & Nilsson 1997; Poschlod *et al.* 1997). This gap in field studies can be explained by the obvious methodological problems. We faced similar problems in our study and conclusions had to be drawn from laboratory floating experiments rather than from field observations.

Considering an average current velocity of about 4–5 km h^{-1} during base flow (and at least 20–30 km h^{-1} during floods), all species classified within groups 2 to 4 will be able to cover large distances over short periods of time floating on the water surface. This holds true even if seeds are not transported within the main channel. These species differ with respect to the average distance transported and thus the likelihood of colonising distant sites. Thus, a classification according to floating ability makes sense. Our seed release experiments show that even species characterised within group 2 are able to cover long distances floating during normal flow (up to 10% recapturerate over a 1 km stretch). During high floods the amount and the range of dispersed seeds must be much higher.

Of all the species studied only *Silene vulgaris* ssp. *glareosa* and *Gypsophila repens* should be classified as non-floaters. However, both species have previously been characterised as typical examples of species dispersed by running water (e.g. Ellenberg 1988). Therefore, the results obtained in this study shed new light on the concept of "alpine-floaters", i.e. plants which are dispersed downstream from higher regions in the Alps and which are dependent on a permanent supply of seeds or vegetative diaspores. The fairly heavy seeds of *Gypsophila repens* and *Silene vulgaris* ssp. *vulgaris* do not support aerial transport. Dispersal on the stream bottom, as postulated for *Impatiens glandulifera* by Lhotska & Kopecky (1966), also appears unlikely, as mechanical forces in moving gravel are very high in alpine streams. One obvious mechanism for seed transport is movement in the water during high floods, when turbulent flow may keep even heavy seeds suspended. Another possibility is dispersal attached to floating islands of litter. A successful dispersal of vegetative parts of the plants has not so far been observed (Bill 1999).

SEED MORPHOLOGY, SEED MASS AND DISPERSABILITY

Our results show once more, that a classification of seed types according to morphological characteristics (as done by van der

Pijl 1982; Müller-Schneider 1986; Willson *et al.* 1990) is insufficient for an ecological assessment of dispersability. An assessment based on morphological criteria alone will tend to underestimate the actual significance of water-linked dispersal and the degree of polychory; for example, the pappus on the seeds studied not only facilitates flying but also drifting and floating (Ridley 1930; Rydin & Borgegard 1991). *Leontodon hispidus* ssp. *hastilis* showed floating in spite of high seed mass; it was represented in the drift samples. Using the pappus as a support structure seeds of *Calamagrostis pseudophragmites* were also able to float. The significance of polychory has been emphasised previously by Ryvarden (1971), Willson (1993), Bakker *et al.* (1996), Danvind & Nilsson (1997) and Bonn & Poschlod (1998).

There are a number of studies looking at the relationship between seed mass and dispersability (e.g. Salisbury 1975; Venable & Brown 1988; Rees 1993; Bakker *et al.* 1996; Westoby *et al.* 1996). In general, seed numbers and the range of dispersal should increase as seed mass decreases. Our results show no correlation between seed mass and dispersability. Seed mass may only provide initial information, since we observed a wide range of average seed mass for species with different floating abilities (cf. Table 4). However, the median for the four groups in Table 4 declined from 0.5 mg seed^{-1} (group 2) to 0.2 mg seed^{-1} (group 3) to 0.1 mg seed^{-1} (group 4).

DISPERSABILITY *VS* OTHER SURVIVAL STRATEGIES IN A DYNAMIC ENVIRONMENT

Besides occasional drought, the high turnover rate of gravel bars is the most important environmental parameter in and along alpine streams. Fenner (1987) and Bakker *et al.* (1996) argued that for plants there is a close relationship between dispersal strategies and disturbance: species in environments characterized by frequent and stochastic changes should have a particularly high ability for long-distance dispersal. Our results show that pioneer species can be dispersed both by wind (Bill 1999) and by running water. Floating in the current of streams seems to be an efficient dispersal mechanism, although it is necessarily downstream and thus unidirectional.

According to Grime (1979), stress-tolerance (which would require an increased seed mass) in combination with high dispersability is rarely found. Similarly, looking at the initial colonisation of volcanic debris, Wood & Del Moral (1987) found that species transported over long distances were not sufficiently stress-tolerant to overcome the difficulties of germination and establishment under unsuitable soil conditions. However, Rydin & Borgegard (1991) emphasized that the negative correlation between seed size and dispersability only holds true for environments which allow no dispersal by running water. Our results confirm this hypothesis. Considering that after flooding soil water supply is sufficient for a short period of time, species with rapid seedling development will be able to establish at favourable microhabitats characterised by high contents of fine sediments. Successful reproduction will not be possible every year and everywhere, but only when and where conditions and site characteristics are favourable (Krasny *et al.* 1988). The probability of successful reproduction may be increased by the extension of periods when ripe seeds are present (Stöcklin & Bäumler 1996). Furthermore, all the species studied in our project are adapted to temporary isolation by long life expectancy (Müller 1995). Long life expectancy is an important property of pioneer plants along alpine streams, distinguishing them from early colonizers in some other environments (e.g. Grime *et al.* 1988; Bonn & Poschlod 1998).

Some authors assume that dispersal via water is an important determinant of plant distribution and abundance on floodplains (Staniforth & Cavers 1976; Nilsson *et al.* 1994; Johansson *et al.* 1996). However, Parker & Leck (1985) and Danvind & Nilsson (1997) did not find a correlation between floating ability and distribution in some species. Most studies also indicate that aquatic dispersal is just one among many other properties which enable survival in pioneer environments along alpine streams (Bill 1998). Other important properties include high regenerative potentials (Krasny *et al.* 1988), plasticity of life cycles (*Hutchinsia alpina*), suitability for wind dispersal (*Calamagrostis pseudophragmites, Erigeron acris* ssp. *angulosus, Petasites paradoxus*), the production of a high number of seeds (*Myricaria germanica, Saxifraga caesia, Silene vulgaris* ssp. *glareosa*), high germination rate and speed (*Dryas octopetala, Hieracium piloselloides, Calamagrostis pseudophragmites, Petasites paradoxus*) or the formation of a seed bank.

The density of seeds in seed banks on gravel bars may be too low to be detected with the current methods of seed bank analysis (Bill 1999). Poschlod *et al.* (1997) were able to confirm the presence of a seed bank for two pioneer species on gravel bars in the upper Loire floodplain. According to comparative studies (Grime *et al.* 1988; Thompson *et al.* 1997) the formation of a short- (st) or long-term (lt) persistent seed bank is likely for *Agrostis gigantea* (st), *Campanula cochleariifolia* (lt), *Dryas octopetala* (st), *Leontodon hispidus* (st), *Poa alpina* (st) and *Silene vulgaris* (st); the formation of a transient seed bank is likely for *Arabis alpina*.

However, the example of the highly endangered plant *Calamagrostis pseudophragmites* (Korneck *et al.* 1996) shows that high seed production, medium germination rates and excellent suitability for dispersal by wind and water are insufficient if hydro-engineering causes the loss of sites suitable for colonization (moist gravel bars with high contents of fine sediment) (Reich & Erber 1999). Reservoirs may also form a barrier for species dependent on water-linked long-distance dispersal (Ellenberg 1988; Johansson *et al.* 1996).

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