



ORIGINAL ARTICLE

Hydrochoric Seed Dispersal of Riparian Plants Follows Hydrological Patterns Closer Than Geomorphic Variation

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ABSTRACT

Water is an important dispersal vector for seeds of riparian plants, but little is known on how this form of dispersal, called hydrochory, varies throughout seasons and through geomorphically different areas. Therefore, we trapped seeds in 25 x 25 Astroturf mats along a free-flowing boreal river for an entire year. Sites mirrored the full range of geomorphic variation in the area and traps were emptied before and after the annual peak flow. The traps collected 2,062 seeds before the spring flood and 16,157 during the spring flood. While most of the seeds were deposited in the summer-low water traps (from now on “water edge”) before the spring flood, they were distributed more equally in the

riparian traps (defined as the level 40 cm above the water edge; from now on “riparian zone”) during the spring flood. We found 77 species in total, of which 71 were at least recorded during the spring flood. Species numbers were higher at the water edge than at the riparian zone before and during the spring flood. Only 6.6% of the seeds, from 26 species, were viable. Most viable seeds were found in the water edge traps and, during the spring flood, in the riparian zone traps. While species that are primarily dispersed by water were not the most abundant among the viable seeds, they were the most species-rich group. This means that hydrochory is an important dispersal mechanism for riparian vegetation and an important contributor to riparian plant diversity in free-flowing rivers, and that changes in flow regimes, such as by flow regulation, can affect riparian vegetation composition.

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Key words: Dispersal; Riparian vegetation; Hydrology; Geomorphology; Seeds; Plant diversity; Germination.

HIGHLIGHTS

- Water is a major dispersal vector for riparian plants, especially during high flows
- Lakes receive more seeds, but not species, than slow-flowing reaches and rapids
- Hydrochory can help maintain taxonomic and functional diversity

INTRODUCTION

Dispersal is one of the main drivers of community and metacommunity dynamics and the process that connects populations with one another (Leibold and others 2004). While dispersal patterns in terrestrial systems can be omnidirectional, such patterns often take a uni- or bidirectional form for species in freshwater ecosystems (Bourgeois and others 2016; Green and others 2022). This is the case especially in narrower and lotic ecosystems, such as streams and rivers, while lentic areas, such as lakes, show more variation in dispersal patterns because of factors such as wind (Sarneel and others 2014). Riparian vegetation commonly depends on water for dispersal (Johansson and others 1996; Moggridge and others 2009), and many of its species have seeds with morphological adaptations that increase buoyancy and postpone germination. Such adaptations include porous tissue or air pockets and impermeable seed coats (Lopez 2001; Merritt and Wohl 2002). Plant reproductive life history strategies can also include adaptations to disperse more effectively, such as synchronisation of seed release with flow events (Blom 1999; Lytle and Poff 2004). Streams have an enormous capacity for dispersal of seeds via water (hydrochory). They can transport large amounts of both generative and vegetative plant propagules (Boedeltje and others 2004; Tabacchi and others 2005), and dispersal distances can be over hundred kilometres in a free-flowing river (Andersson and others 2000).

Free-flowing rivers often display a flow regime with one or more peak flows that are important for seed dispersal and riparian vegetation composition (Nilsson and others 2010). Peak flows are characterised by higher numbers of entrained seeds than during lower flows (Boedeltje and others 2004; Moggridge and Gurnell 2010), and the seeds that they deposit codetermine the composition of local riparian vegetation throughout the growing season (Fraaije and others 2015a; Sarneel and others 2016). Deposition patterns reflect plant adaptations to hydrochory and the flow regime. For example,

floral communities in riparian zones are often stratified by elevation such that they reflect the buoyancy of seeds (Fraaije and others 2017) and preferences for soil moisture content (Fraaije and others 2015b). This implies that hydrochory is an important factor in riparian vegetation dynamics.

Dispersal and species composition in and along rivers was initially mostly studied along a longitudinal gradient (Bendix 1994; Vannote and others 1980). More recently, attention to network structure (Brown and Swan 2010; Kuglerová and others 2015; Tonkin and others 2018) and local geomorphic heterogeneity (Fraaije and others 2017; Jähnig and others 2009; Su and others 2019) has increased, as has the attention to plant functional traits (Merritt and others 2010a; Nilsson and others 2002). Drawing from patch dynamics theory, Montgomery (1999) formulated the Process Domain Concept to describe geomorphic variation. According to this concept, river process domains (RPDs) are geomorphically distinct stretches of systems, upon which peak flows act as a disturbance with a certain frequency, magnitude and duration. RPD characteristics include valley geometry, channel sinuosity, slope and width, bank steepness and bed grain size. These factors shape disturbances such as floods, and by extension their impact on riverbanks. High flow velocity, for example, can scour away vegetation and entrain sediment and propagules. The impact of this flow velocity will vary: in steep channels with coarse substrates, it will likely result in more entrainment than in wide channels. Similarly, both flow velocity and hydraulics play a role in seed deposition (Merritt and Wohl 2002), resulting in spatially heterogeneous seed deposition patterns among RPDs (Su and others 2019). Additionally, species with different buoyancy are affected differently by these conditions (Nilsson and others 2002). Short-floating species are more likely to sink to the bottom than to be deposited at the water edge under low-flow conditions, leading to an increase in their proportions in the riparian vegetation with increasing flow velocity. These differences in deposition patterns, combined with differences during seed germination and seedling recruitment, can result in distinct species communities in different RPDs (Bendix and Hupp 2000; Polvi and others 2011).

To better understand the first stages of riparian vegetation community assembly, we analysed year-round seed deposition through hydrochory in sites covering the full range of geomorphic variation in a free-flowing boreal river. To our knowledge, we are the first to collect such a dataset,

analyse it on the species level, assess seed viability as well as analyse seed functional composition with regard to dispersal mechanisms. In free-flowing boreal riverscapes, the spring flood is the largest peak flow and the main hydrological event. To understand the importance of the spring flood, we compared the numbers and composition of seeds deposited during this period to those during the rest of the year. We analysed the viable fraction of the deposited seeds through a germination experiment and used dispersal traits to analyse the taxonomic and functional composition of the viable seeds. We expected (Hypothesis 1) higher numbers of deposited seeds and species during the spring flood than during the rest of the hydrological year. We expected to see (Hypothesis 2) that seeds are deposited at the water edge year-round and in the riparian zone after the spring flood, but not in the riparian zone before the spring flood. Geomorphic variability in the study system is captured by the following types of process domains: lakes, slow-flowing reaches and rapids. We expected the degree of hydrological disturbance at different RPDs to result in (Hypothesis 3) negative correlations between flow velocity and numbers of deposited seeds and species, that is, highest numbers in lakes, intermediate numbers in slow-flowing reaches and lowest numbers in rapids. These hypotheses were first tested for all seeds trapped in the experiment, and then for the viable subset. We analysed the functional composition of the viable subset and expected to find (Hypothesis 4) relatively more long-floating seeds in slow-flowing reaches and lakes than in rapids. Among the viable seeds, we expected (Hypothesis 5) relatively more hydrochoric seeds and species during the spring flood than during the rest of the year.

METHODS

Study Site

We conducted a seed trapping experiment along the streambanks and floodplains of Hjuksån, a free-flowing tributary to the Vindel River in northern Sweden (Figure 1a). During the first part of the twentieth century, large parts of Hjuksån were channelised for timber-floating. Some of these structures, such as dams and canals, still exist but are not maintained, and some reaches have been restored to increase geomorphic complexity (for example, Gardeström and others 2013). The northern Swedish landscape is characterised by relatively low relief shaped by multiple continental glaciations and remains in isostatic rebound from

the latest glaciation (Polvi and others 2014). The main RPD types in tributaries to large rivers in the area are lakes, slow-flowing reaches and rapids that alternate with each other in free-flowing catchments. These three RPDs represent hydrogeomorphic gradients with increasing bed slope, substrate coarseness and hydraulic complexity, respectively (Polvi and others 2014; Su and others 2019). Hjuksån's flow regime is dominated by a peak flow from snow- and ice-melt in the late spring (May–early June). Flow is lower in the summer, increases with precipitation events in autumn and is usually lowest in the winter because of the river freezing over, except during ice-induced winter floods. Vegetation in the uplands consists of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) with undergrowth of *Vaccinium* spp. Riparian vegetation is rich in graminoids such as *Carex* spp., herbs and shrubs such as *Salix* spp.

Field Experiment

To address the five hypotheses presented above, seed traps were placed in the riparian zone of twelve sections of Hjuksån: four lakes, four slow-flowing reaches and four rapids (Figure 1b). Traps were placed along five transects perpendicular to the channel, each consisting of two plots: one right at the summer-low water edge and one at 40 cm above the low water surface elevation, in the riparian zone (Figure 1c). The 40 cm elevation was taken as the vertical elevation, which means that over-land distances can vary between transects. Transects were placed 10 metres from each other, which was the maximal possible distance in the (short) rapids. Seeds were trapped using 25 x 25 cm Astroturf seed traps with tent pegs in each corner (Wolters and others 2004). The first batch of traps was placed after the 2017 spring flow, from 10 to 20 June until 21 August–1 September 2017. This batch contained 120 traps with seeds of the season or seeds dispersed to the area by base flow. Directly after and after the peak of the growing season, from 21 August–1 September 2017, a second batch of traps was placed in the exact same places as the first and left over winter. As the catchment freezes over during winter, dispersal is virtually impossible and so this second batch, that was harvested between 18 June and 3 July 2018, resulted in 120 traps that include the seeds deposited by the spring peak flow of 2018. This two-batch design allows for an ecologically appropriate comparison of local seed production and seed deposition by base flow (batch I) and seed deposition by the peak flow (batch II).

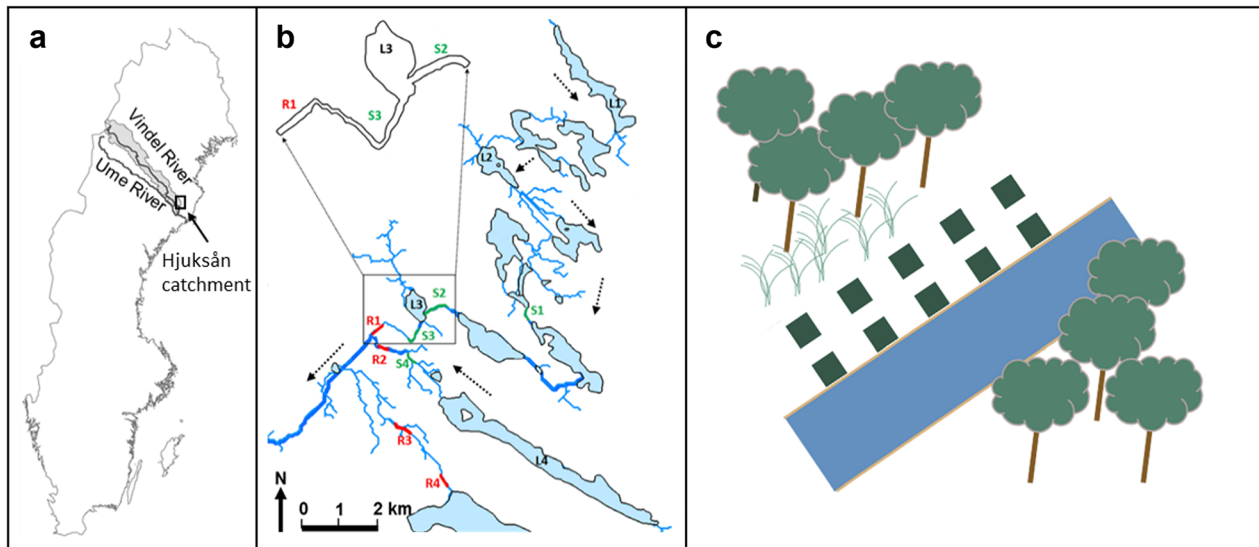


Figure 1. Location of the Hjuksån catchment in Sweden (**a**), the distribution of the different sites in the catchment (**b**, L = lake, S = slow-flowing, R = rapid) and conceptual overview of the distribution of plots per site (**c**) over two elevations (the water edge and 40 cm vertically above the waterline, the riparian zone).

We retrieved a total of 240 traps but removed two from the dataset as they were found upside down. Four other traps had moved but were still pinned in at least one corner and were therefore kept for further analysis. Seed traps were stored cold (+4 °C) and dark until further processing in the laboratory. There, we flushed the traps with water and wet-sieved (0.1 mm) them to extract all deposits. Seeds in the deposits were identified based on a large photograph collection (Cappers and others 2012), to the lowest possible taxonomic level, following Krok and Almquist (2013), and stored dry and in room temperature.

Germination Experiment

Starting in 2019, we conducted a germination experiment on all seeds to test for viability. The seeds were planted individually by placing them on moist potting soil (EC 1-2, pH 5.5-6.5) after which they were kept in cold stratification (+4 °C) to break dormancy. Seeds were in stratification for at least two months, and out for germination for 60 days. Due to the large number of seeds, the germination experiment was divided into eleven batches. Consecutive batches of trays with seeds were in stratification between July 2019 and February 2022, and out for germination between January 2020 and April 2022. We saw no correlation between seed longevity or stratification duration, and germination success (data not shown).

The germination experiment took place in a plant growing room with 18 hours of light per day

(Philips TL5 HE 28W 830 (MASTER), 2625 lm), daily watering and a temperature of 22–25 °C. Trays were rotated, and seeds were checked for radicle extrusion every third day; these dates were assumed to be the day of germination. Seedlings were removed when they started to overshadow other seeds and potted for further identification if they were seeds of unknown species. Seeds of four *Carex* and three *Salix* species as well as a grass species could not be identified to the species level, and seeds of four other species could not be identified at all. These were named *Carex* Sp1, *Carex* Sp2, and so on, Poaceae, and Sp1, Sp2, and so on, respectively.

Analyses

To assess whether numbers of trapped seeds and species varied over time and the geomorphic gradient, we used generalised linear mixed models (GLMMs). Model selection started with all combinations of interacting variables: timing (pre-spring flood/spring flood), elevation (0/40 cm) and river process domain (lake/slow-flowing/rapid). These variables were all categorical, and sites were always included as a random effect. GLMMs were run with a negative binomial distribution to account for overdispersion in the data, and final models (Table 1) were selected based on lowest AIC. We also analysed the numbers of germinated seeds with GLMMs and did not analyse patterns of germinated species as numbers were too low. GLMMs were calculated with package *lme4* (v1.1-35.3; Bates and

Table 1. Characteristics of Final GLMMs

Model name	Response variable	Fixed effects	Random effects	Pseudo- R^2 (marginal)	Pseudo- R^2 (conditional)	ICC
GLMM1	Number of stranded seeds	Timing + RPD + Elevation + Timing $\times$ RPD + Timing $\times$ Elevation + RPD $\times$ Elevation	Location	0.618	0.751	0.347
GLMM2	Number of stranded species	Timing $\times$ Elevation	Location	0.571	0.639	0.159
GLMM3	Number of germinated seeds	Timing $\times$ Elevation	Location	0.147	0.438	0.342

Marginal pseudo- R^2 values are based on the fixed effects, conditional pseudo- R^2 values include random effects (that is, site), ICC is intraclass correlation coefficient.

others 2024), and we used package *MuMIn* (v1.47.4; Bartón 2023) for model selection, package *emmeans* (v1.10.1; Lenth and others 2024) to further analyse contrasts between variables and package *performance* for pseudo- R^2 and ICC calculations (v0.11.0; Lüdtke and others 2021), in R (v4.3.3; R Core Team 2023).

Seed trait data on dispersal mechanisms were retrieved from Tyler and others (2021) and on seed buoyancy from Andersson and others (2000), Danvind and Nilsson (1997) and Romell (1938). Community-weighted means (CWMs) were calculated based on quantitative data on floating time, which were available for 17 species. Species were categorised as long- or short-floating species (data available for 19 species, divided in floating time longer or shorter than two days, following Andersson and others 2000) for visualisation of floating capacity.

RESULTS

In total, the seed traps caught 18,219 seeds of 77 species during one year in Hjuksån's riparian zones (Table 2), of which 16,157 seeds (88.7 %) were dispersed during the spring flood. Out of 77 trapped species, 63 could be identified to the species level. All of these were native species, except for the non-invasive species *Brassica rapa* (Tyler and others 2021). Of the 63 species, 45 (71.4 %) were also found in a vegetation inventory that was carried out in the same catchment in 2017 and contained 127 plant species that reproduce by seeds (L.E. Polvi, unpubl. data). From the 120 traps that were out during the pre-spring flood period, seven traps caught zero seeds. During the spring flood period, one trap out of 118 caught zero seeds.

We found that seeds were not deposited equally through time or space and that variation within and between RPDs was quite large (Figure 2a). Per trap, more seeds were deposited during the spring flood than during the rest of the year (Hypotheses 1+2; Table 3, model summary in Table S1 and interaction plot in Figure S1), at both the water edge (est. 1.43, $p < 0.001$) and in the riparian zone (est. 2.96, $p < 0.001$). The same pattern was found for the number of deposited species (Hypotheses 1+2; Figure 2b) on the water edge (est. 0.994, $p < 0.001$) and in the riparian zone (est. 1.238, $p < 0.001$), although differences were smaller (Table 4, model summary in Table S2 and interaction plot in Figure S2). The higher seed deposition during the spring flood could be seen in all process domains (Hypothesis 3; all est. ≥ 1.86 , all p values < 0.001). Unlike slow-flowing reaches and rapids, lakes had higher seed deposition at the water edge than in the riparian zone (Hypotheses 2+3; est. 1.396, $p < 0.001$).

Viable Seeds

Over the course of the germination experiment, 6.58% of the seeds germinated, adding up to a total number of 1,199 germinated seeds of 26 species (Table 2). Of the viable species that could be identified to the species level, all but *Viola tricolor* occurred in the vegetation as surveyed in the catchment in 2017 (L.E. Polvi, unpubl. data). Numbers of viable seeds per trap were highly variable (Figure 3a). We found that water deposits viable seeds equally year-round (Hypothesis 1; Table 5, model summary in Table S3 and interaction plot in Figure S3). Looking at all RPDs simultaneously, numbers of viable seeds were higher on the water edge than in the riparian zone before the

Table 2. List of Species Trapped in Seed Traps Along Hjuksån (Sweden) During 2017–2018

Species name	Number of trapped seeds	Number of germinated seeds	Germination (%)
<i>Achillea ptarmica</i>	1	0	–
<i>Agrostis canina</i>	72	0	–
<i>Agrostis gigantea</i>	14	0	–
<i>Alnus incana</i>	598	13	2.2
<i>Angelica sylvestris</i>	6	0	–
<i>Betula</i> spp.	13,048	872	6.7
<i>Brassica rapa</i>	75	0	–
<i>Calamagrostis canescens</i>	20	0	–
<i>Calamagrostis epigejos</i>	73	0	–
<i>Calamagrostis purpurea</i>	7	0	–
<i>Calamagrostis stricta</i>	1	0	–
<i>Calluna vulgaris</i>	55	7	12.7
<i>Carex acuta</i> *	228	18	7.9
<i>Carex aquatilis</i> *	3	0	–
<i>Carex buxbaumii</i> *	1	0	–
<i>Carex canescens</i> *	257	199	77.4
<i>Carex chordorrhiza</i> *	9	1	11.1
<i>Carex dioica</i> *	13	1	7.7
<i>Carex flava</i> *	133	3	2.3
<i>Carex lasiocarpa</i> *	267	1	0.4
<i>Carex limosa</i> *	1	0	–
<i>Carex loliacea</i> *	5	0	–
<i>Carex magellanica</i> *	7	1	14.3
<i>Carex nigra</i> *	350	16	4.6
<i>Carex panicea</i>	1	0	–
<i>Carex rostrata</i> *	403	11	2.7
<i>Carex</i> Sp1	3	0	–
<i>Carex</i> Sp2	2	0	–
<i>Carex</i> Sp3	29	1	3.5
<i>Carex</i> Sp4	225	1	0.4
<i>Carex vesicaria</i> *	546	6	1.1
<i>Cicuta virosa</i>	1	0	–
<i>Cirsium palustre</i>	1	0	–
<i>Comarum palustre</i>	154	8	5.2
<i>Eleocharis mamillata</i>	1	0	–
<i>Eleocharis palustris</i>	2	0	–
<i>Elytrigia repens</i>	10	0	–
<i>Empetrum nigrum</i>	34	0	–
<i>Festuca ovina</i>	8	0	–
<i>Festuca pratensis</i>	115	0	–
<i>Filipendula ulmaria</i>	250	7	2.8
<i>Fragaria vesca</i>	2	0	–
<i>Geranium sylvaticum</i>	2	1	50.0
<i>Juncus filiformis</i>	6	2	33.3
<i>Luzula multiflora</i>	1	0	–
<i>Menyanthes trifoliata</i>	22	0	–
<i>Molinia caerulea</i>	449	0	–
<i>Nuphar lutea</i> *	2	0	–
<i>Nymphaea alba</i> *	11	0	–
<i>Paris quadrifolia</i>	1	0	–
<i>Pedicularis palustris</i>	11	0	–
<i>Peucedanum palustre</i>	1	0	–
<i>Phragmites australis</i>	40	0	–

Table 2. continued

Species name	Number of trapped seeds	Number of germinated seeds	Germination (%)
<i>Picea abies</i>	64	1	1.6
<i>Pinus sylvestris</i>	134	9	6.7
<i>Poa nemoralis</i>	7	0	–
<i>Poa palustris</i>	1	0	–
<i>Poa trivialis</i>	62	0	–
Poaceae	3	0	–
<i>Potamogeton alpinus*</i>	1	0	–
<i>Potamogeton natans*</i>	6	0	–
<i>Potamogeton perfoliatus*</i>	1	0	–
<i>Rubus idaeus</i>	6	0	–
<i>Salix</i> Sp1	3	0	–
<i>Salix</i> Sp2	1	0	–
<i>Salix</i> Sp3	1	0	–
<i>Scutellaria galericulata</i>	4	0	–
<i>Trichophorum cespitosum</i>	1	0	–
<i>Vaccinium myrtillus</i>	4	0	–
<i>Vaccinium</i> sp.	12	2	16.7
<i>Valeriana sambucifolia</i>	9	2	22.2
<i>Viola palustris</i>	57	4	7.0
<i>Viola tricolor</i>	30	3	10.0
Sp1	231	9	3.9
Sp2	1	0	–
Sp3	1	0	–
Sp4	2	0	–

Species that are deemed hydrochoric by Tyler and others (2021) are marked with “*”. Per species, the number of trapped seeds and viable fraction are given. Species with 0 germinated seeds have a reported germination percentage of “–”.

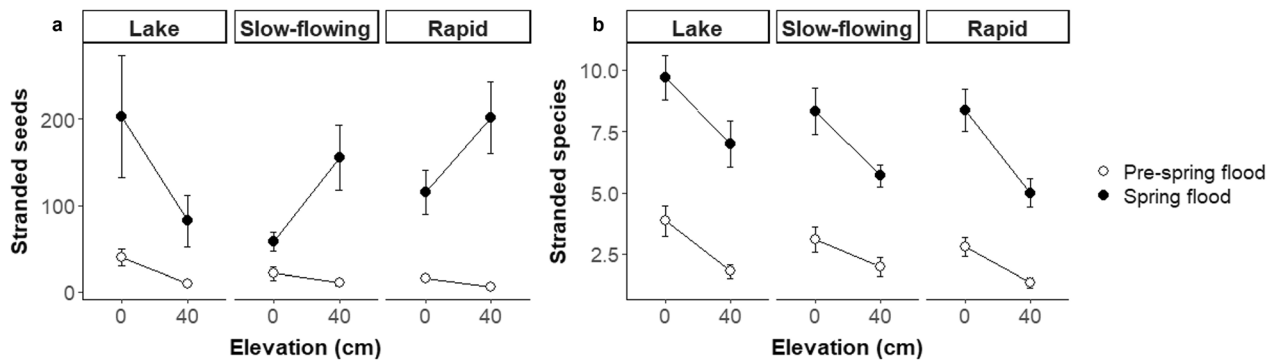


Figure 2. Mean ($\pm$ SE) of numbers of seeds (a) and plant species (b) caught in seed traps in the riparian zone of Hjuksån before the spring flood (early–late summer 2017) and during the spring flood (late summer 2017–early summer 2018).

spring flood (Hypotheses 2+3; est. 1.253, $p < 0.001$). Numbers of viable seeds were overall higher during the spring flood, and mainly deposited in the riparian zone. Due to the low numbers of species, germination patterns on the species level (Figure 3b) were unsuitable for further analysis.

Functional Trait Analysis

Only seeds that proved viable in the germination experiment were included in functional trait analyses. Trait data related to buoyancy were available for 19 (qualitatively) and 17 (quantitatively) species, and on seed dispersal for 22 species. Seeds

Table 3. Contrasts Calculated with GLMM1 ($n = 18,219$ seeds)

Contrasts	Estimate	SE	z ratio	p
Timing × Elevation				
<i>0 cm</i>				
Pre-spring flood–Spring flood	−1.43	0.180	−7.92	<.001
<i>40 cm</i>				
Pre-spring flood–Spring flood	−2.96	0.186	−15.901	<.001
<i>Pre-spring flood</i>				
0 cm–40 cm	1.261	0.186	6.775	<.001
<i>Spring flood</i>				
0 cm–40 cm	−0.267	0.177	−1.507	ns
RPD × Elevation				
<i>0 cm</i>				
Lake–Slow-flowing	1.018	0.464	2.192	ns
Slow-flowing–Rapid	−0.237	0.466	−0.509	ns
Lake–Rapid	0.781	0.464	1.682	ns
<i>40 cm</i>				
Lake–Slow-flowing	−0.507	0.467	−1.085	ns
Slow-flowing–Rapid	0.117	0.466	0.251	ns
Lake–Rapid	−0.390	0.467	−0.834	ns
<i>Lake</i>				
0 cm–40 cm	1.396	0.220	6.335	<.001
<i>Slow-flowing</i>				
0 cm–40 cm	−0.129	0.222	−0.582	ns
<i>Rapid</i>				
0 cm–40 cm	0.225	0.220	1.026	ns
Timing × RPD				
<i>Pre-spring flood</i>				
Lake–Slow-flowing	0.381	0.469	0.812	ns
Slow-flowing–Rapid	0.202	0.470	0.430	ns
Lake–Rapid	0.583	0.468	1.245	ns
<i>Spring flood</i>				
Lake–Slow-flowing	0.130	0.465	0.280	ns
Slow-flowing–Rapid	−0.322	0.465	−0.692	ns
Lake–Rapid	−0.192	0.464	−0.414	ns
<i>Lake</i>				
Pre-spring flood–Spring flood	−1.86	0.223	−8.344	<.001
<i>Slow-flowing</i>				
Pre-spring flood–Spring flood	−2.11	0.231	−9.112	<.001
<i>Rapid</i>				
Pre-spring flood–Spring flood	−2.63	0.220	−11.962	<.001

Contrasts between combinations of timing, elevation and river process domain, as included in GLMM1 ($n = 18,219$ seeds). Results are given on the log scale. “ns” indicates non-significant (with $\alpha = 0.05$).

dispersed during the spring flood generally had lower dispersal capacity (Hypothesis 4; community-weighted means, Figure 4) than those dispersed before the spring flood, but there was substantial variation between sites and RPDs. These differences and those between the two elevations were not consistent. RPDs received similar numbers of long-floating species, and barely any short-floating species during the spring flood (Figure S4). The highest number of long-floating species were deposited on the water edge of lakes before the spring flood,

where most (viable) seeds were deposited during that period of time (Figures 2a and 3a), and in the riparian zones of lakes during the spring flood.

Most of the viable seeds (Figure 5a) that we found were of species with adaptations to wind-assisted dispersal. The majority of these were seeds of *Betula* spp., which made up 72.7% of all viable seeds. The second-most abundant species in the viable fraction of the dataset was *Carex canescens*, a hydrochoric species. Many other *Carex* species are also hydrochoric and contributed to the relative

Table 4. Contrasts Calculated with GLMM2 ($n = 77$ species)

Contrasts	Estimate	SE	z ratio	p
Timing × Elevation				
0 cm				
Pre-spring flood–Spring flood	−0.994	0.0965	−10.303	<.001
40 cm				
Pre-spring flood–Spring flood	−1.238	0.1213	−10.208	<.001
Pre-spring flood				
0 cm–40 cm	0.639	0.130	4.900	<.001
Spring flood				
0 cm–40 cm	0.395	0.084	4.716	<.001

Contrasts between combinations of timing and elevation, as included in GLMM2 ($n = 77$ species). Results are given on the log scale. “ns” indicates non-significant (with $\alpha = 0.05$).

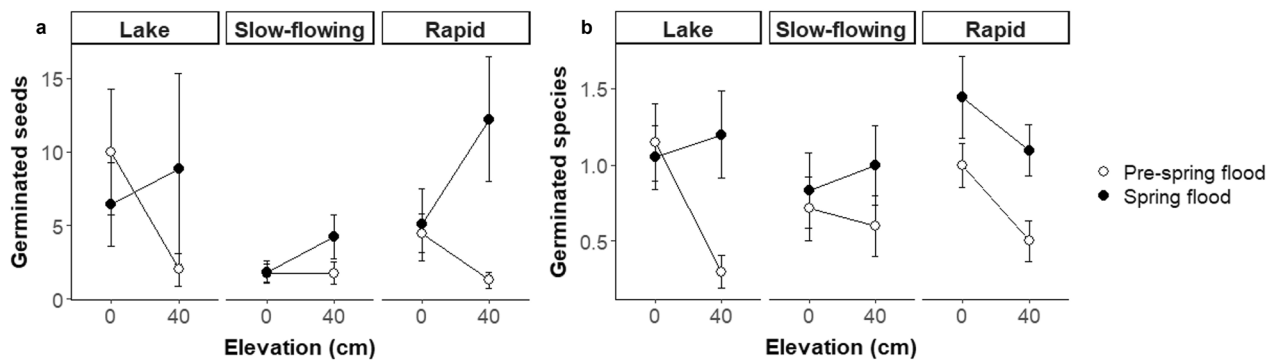


Figure 3. Mean ($\pm$ SE) of numbers of seeds (**a**) and plant species (**b**), originally caught in seed traps in the riparian zone of Hjuksån, that were deemed viable through an indoors germination experiment.

Table 5. Contrasts Calculated with GLMM3 ($n = 1,199$ viable seeds)

Contrasts	Estimate	SE	z ratio	p
Timing × Elevation				
0 cm				
Pre-spring flood–Spring flood	0.28	0.324	0.865	ns
40 cm				
Pre-spring flood–Spring flood	−1.55	0.334	−4.638	<.001
Pre-spring flood				
0 cm–40 cm	1.253	0.334	3.749	<.001
Spring flood				
0 cm–40 cm	−0.576	0.319	−1.807	ns

Contrasts between combinations of timing and elevation, as included in GLMM3 ($n = 1,199$ viable seeds). Results are given on the log scale. “ns” indicates non-significant (with $\alpha = 0.05$).

high numbers of hydrochoric species among the viable seeds. Water-dispersed seeds did occur in all types of RPDs and both before and during the spring flood.

Compared to the numbers of seeds, there were more water-dispersed species than species with other dispersal mechanisms (Figure 5b). We found

that fewer seeds, but more unique water-dispersed species were deposited during the spring flood (Hypothesis 5; 10 species, 49 seeds) than pre-spring flood (5 species, 208 seeds).

DISCUSSION

Hydrochory is a key process underlying community composition of riparian vegetation. In this study, we found that free-flowing rivers transport most seeds during the annual peak flow, and that geomorphic variation has some, but a smaller, effect on seed deposition patterns. Only a minor portion of the dispersed seeds are viable, which corroborates previous studies (Nilsson and Grelsson 1990; Vogt and others 2006). The deposited seeds reflected the catchment's vegetation (L.E. Polvi, unpubl. data)

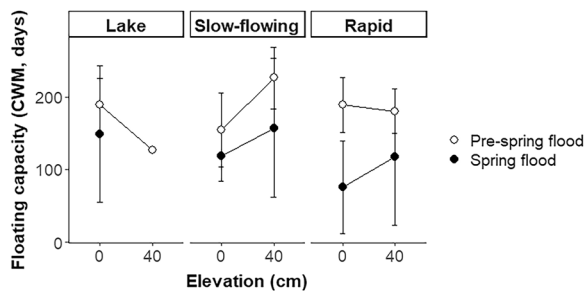


Figure 4. Community-weighted means (CWM) and standard deviations (CWSD) of seed buoyancy in days (Andersson and others 2000), based on the viable seeds of 17 species.

and represented a wide variety of dispersal mechanisms.

Temporal and Geomorphic Variation in Seed Deposition

Our results demonstrated that all RPDs received significantly more seeds and species during the spring flood than during the rest of the year (Figures 2 and 3), which supports Hypothesis 1. The difference in numbers of deposited seeds cannot be explained by length of the trapping period: despite this period being longer for the spring flood traps, the traps and the catchment were covered in snow and ice for most of this time, making it hard for seeds to be transported, and almost impossible for them to be deposited (Nilsson and others 2010). The result that seeds from significantly more species were deposited during the spring flood than before (71 vs. 39), is similar to findings in other climates and on different spatial scales (Boedeltje and others 2004; Moggridge and others 2009; Qian and others 2024). The similar difference in the subset of viable seeds (24 vs. 14) illustrates the importance of hydrochory as a contributor to riparian plant diversity.

The seasonal difference in seed deposition was particularly evident in slow-flowing reaches and rapids, but we found that differences between RPDs

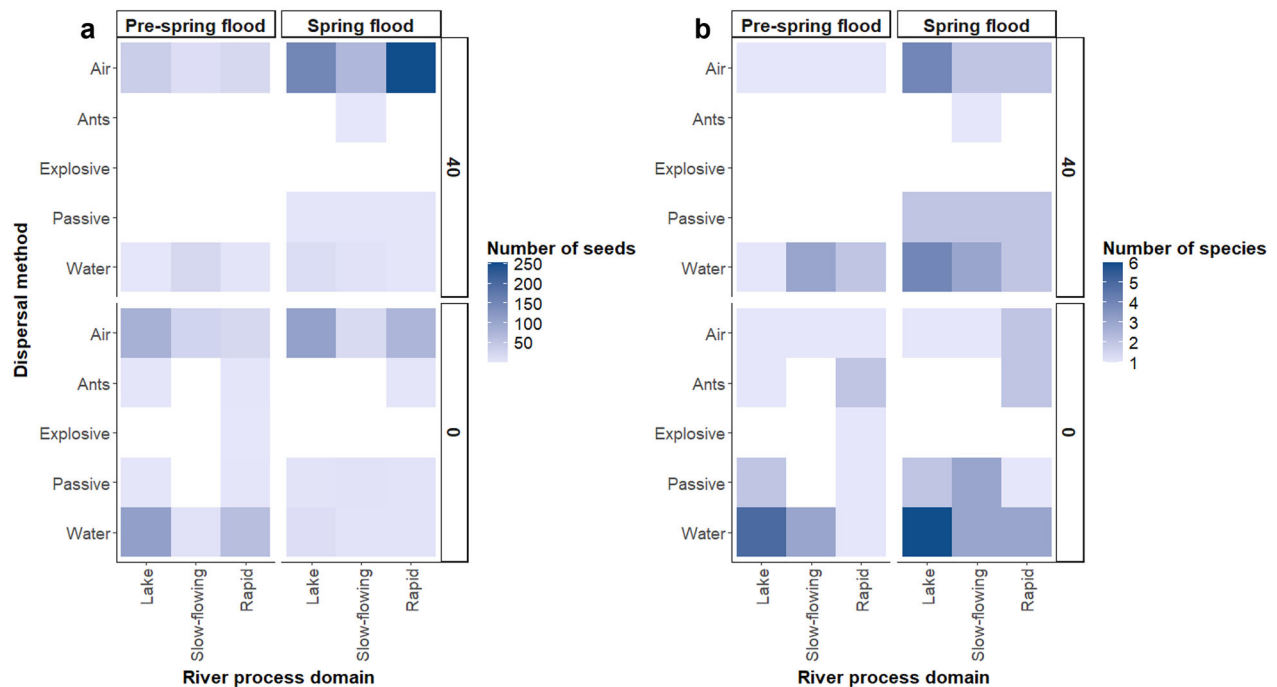


Figure 5. Numbers of viable seeds (a) and viable species (b) that stranded during the experiment. They are categorised according to dispersal mechanism (Tyler and others 2021), river process domain, elevation in the riparian zone (0 or 40 cm) and timing (pre-spring flood and spring flood).

were smaller than expected (Hypothesis 3). Seasonal differences in numbers of viable deposited seeds between RPDs were not tested for (GLMM3) but seemed slightly more pronounced in slow-flowing reaches and rapids, especially in the riparian zone (Figure 3a). Because numbers of deposited propagules were positively correlated to local species richness of riparian vegetation (Andersson and others 2000), changes in timing or magnitude of the spring flood may affect the vegetation along these RPDs more than that of lake banks. Changed timing of peak flows can lead to phenological mismatches in seed entrainment and deposition (Greet and others 2011; Lytle and Poff 2004; Sarnéel and others 2016), while decreased magnitude may lead to deposition less far on the banks and narrower riparian zones (Ström and others 2012). These narrower riparian zones will lead to changes in riparian vegetation composition through habitat loss because of changed hydro-environmental heterogeneity, and increased competition for space (Connor and McCoy 1979; Jansson and others 2019). The boreal spring flood mostly transports seeds from the previous season, and an earlier onset of hydrochory may lead to increased seed mortality and decreased germination success due to seed deposition during unsuitable conditions (Guilloy-Froget and others 2002), which will affect species that depend on hydrochory for their dispersal more than others. Both flow regulation, a widely occurring practice in the boreal zone, and the changing climate affect these peak flow characteristics (Arheimer and others 2017; Hoppenreijs and others 2022; Jansson and others 2019). Through their dependence on the spring flood, slow-flowing reaches and rapids may be especially affected.

The finding that traps in the riparian zone trapped fewest seeds and species before the spring flood confirmed Hypothesis 2. We, however, also found that lakes consistently received more seeds at the water edge than in the riparian zone, which may have been caused by two factors. First, due to the open character of lakes, wind plays a larger role in transporting seeds towards the riparian zone there than in slow-flowing reaches and rapids (Su and others 2019), especially during low-flow conditions. Second, lakes often have more gently-sloping banks, facilitating deposition during the descending limb of the peak flow hydrograph more than along steep streambanks. Moggridge and Gurnell (2010) also found higher numbers of water-dispersed propagules at low elevations of sites with gentler slopes but reasoned that this could also be related to flow restriction by a weir downstream of these

sites. We did not measure bank slope in this study and observed large variation in slope morphology within all three process domains. We hypothesise that, in our study, wind has affected seed stranding patterns more than bank slopes.

The overlap in composition of deposited seeds and the catchment's vegetation, as well as the large number of lakes present in the area (Figure 1) which may hamper long-distance dispersal (Ward and Stanford 1983), make it hard to discern the exact roles that local and regional sources play in plant dispersal. Many of the viable species in the pre-spring flood subset were typical hydrochoric species. Their seeds may have been sourced locally, but can also have been re-dispersed from upstream in the catchment (Nilsson and others 2010), which suggests that hydrochorically dispersed seeds can remain viable for more than one "dispersal season". Comparison of seed trap contents with the vegetation directly surrounding the trap could help confirm or rule out the possibility of local sourcing, as well as that of re-dispersal and other, non-hydrochory dispersal mechanisms.

Functional Composition of Viable Seeds

Viable seeds deposited at lake shores were dominated by long-floating species (that is, floating capacity of more than two days), while the proportions were more similar at slow-flowing reaches and rapids (Figure S4). This partially supports Hypothesis 4 and is corroborated by findings from Nilsson and others (2002), who reported higher proportions of species with long-floating propagules in the riparian vegetation of lakes than for lotic habitats. Most likely, short-floating seeds in lakes sink before they reach the lakeshore. Community-weighted means of floating capacity did not show a consistent pattern across RPDs, but seeds deposited during the spring flood tended to have lower floating capacity than those deposited before (Figure 4).

We expected that both the number of hydrochoric seeds and that of hydrochoric species would be higher during the spring flood but found no support for the first part of this hypothesis (Hypothesis 5, Figure 5). Numbers of hydrochoric seeds usually decrease with distance from the waterline (Fraaije and others 2017; Merritt and Wohl 2006); however, we did not find a similar pattern on the two elevations included in this study, which may be due to the spatial scale on which the seed traps were placed. A finer resolution of seed traps and an extension of the transect

towards the upland would likely have resulted in a gradual decrease of hydrochoric species.

Considering all dispersal mechanisms simultaneously (Tyler and others 2021), we found more mechanisms represented in the deposits of the spring flood than in those collected before the spring flood (Figure 5). This increased functional dispersal diversity aligns with the theory that species may use multiple mechanisms for dispersal (Catford and Jansson 2014; Danvind and Nilsson 1997) and that high flows support weak dispersers (Qian and others 2024). The quantity of seeds of hydrochoric species was not higher during the spring flood than before. In contrast, the number of species was higher, which suggests that these species do not only use water as a vector but depend on the spring flood for their dispersal. Many hydrochoric species do not use other vectors for their dispersal (Merritt and others 2010a) and may thus be affected disproportionately by changes in the natural flow regime that affect the spring flood.

While we cannot completely exclude the possibility of seeds landing in traps by other means than water, we conclude from the low numbers of seeds, species and viable seeds in the traps on 40 cm elevation that were placed before the spring flood, that our experiment was successfully collecting hydrochoric deposits, and that depositions from other sources were relatively rare. This implies that species that are not typically seen as hydrochoric also get transported by water. These species, such as *Betula* spp., were deposited along with more typical hydrochoric species, despite not having typical morphological adaptations for this kind of dispersal. Nilsson and others (2010) already acknowledged that other dispersal mechanisms contribute propagules to rivers, making hydrochory one of multiple steps in the dispersal process. The present study does not provide a full understanding of whether hydrochory is the only, the first or a later step in the dispersal process of species that are usually associated with other dispersal mechanisms. It does, however, support the suggestion that hydrochory supports dispersal of a wide variety of species, which can be especially relevant for species that have limited dispersal capacity otherwise (Qian and others 2024).

Concluding Remarks

Hydrochory is an important dispersal mechanism for riparian plants, and hydrological variation over time explains seed deposition in the riparian zone better than geomorphic variation. Numbers of dispersed and deposited seeds were almost eight times

higher during the spring flood than the rest of the year and the spring flood deposits seeds far into the riparian zone, especially in slow-flowing reaches and rapids. The contrast between deposits during the spring flood and during the rest of the year is smaller on lake banks, where we observed year-round seed deposition or stranding.

While plant species are often categorised as depending on one dispersal mechanism, we found a high diversity of dispersal mechanisms in our seed traps. This suggests that changes in the flow regime will not only affect species that are usually considered as hydrochoric, but many other species as well. This emphasises the potential of environmental flows (e-flows) and hydrochory as a restoration tool (Hyslop and Trowsdale 2012; Merritt and others 2010b), especially in areas such as the one studied here, where the vegetation, and thus the seed sources, remains largely or entirely native (Dynesius and others 2004). Seed input can be a limiting factor for riparian vegetation composition (Araujo Calçada and others 2015; Brederveld and others 2011) and e-flows that disperse hydrochoric and other species have the potential to increase functional diversity (Qian and others 2024) and improve riparian functioning over the entire geomorphic spectrum.

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DATA AVAILABILITY

Data on trapped seeds and germination is available on Zenodo via <https://zenodo.org/records/14524460>.

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