

Hydrochory increases riparian plant species richness: a comparison between a free-flowing and a regulated river

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Summary

1 The importance of dispersal for plant community structure is poorly understood. Previous studies have hypothesized that patterns in the distribution and genetic structure of riparian plant communities were caused by hydrochory, i.e. plant dispersal by water. We separated the relative contributions of propagules from hydrochory and other dispersal vectors by comparing colonization in pairs of plots, one subject to flooding and deposition of hydrochores and the other unflooded.

2 The number of colonizing individuals and the mortality rate of individuals per year did not differ significantly with flooding, but hydrochory increased the number of colonizing species per year and plot by 40–200%. The pool of colonizing species was 36–58% larger per year for flooded than for unflooded plots, indicating that hydrochory increased the diversity by facilitating long-distance dispersal. Hydrochory resulted in more diverse plant communities after 3 years of succession at both plot and reach scales, despite the fact that flooding caused plant mortality.

3 We found no evidence that dams reduce the abundance and diversity of water-dispersed propagules by acting as barriers for plant dispersal. The role of hydrochory for plant colonization was similar between a free-flowing and a regulated river, although in fragmented rivers propagule sources are likely to be more local (within-impoundment).

4 We conclude that plant dispersal by water, as well as fluvial disturbance, is important for enhancing species richness in riparian plant communities. As flowing water may carry buoyant seeds long distances, riparian plant communities may receive a comparatively large proportion of their seeds by long-distance dispersal.

Key-words: dams, fragmentation, hydrochory, riparian vegetation, river continuum, seed dispersal, seed germination, Sweden, vascular plants, vegetative dispersal

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Introduction

Although dispersal is generally believed to set the template from which community patterns develop, its importance for the structure of most plant assemblages is poorly understood (Levine & Murrell 2003). Many communities are recruitment limited (Menge 1991; Tilman 1994; Turnbull *et al.* 2000), so such information is needed (Levine & Murrell 2003), especially for sessile organisms like plants. Numerous lines of correlative evidence suggest that hydrochory, i.e. dispersal by

water, is important for the distribution (Schneider & Sharitz 1988; Johansson & Nilsson 1993; Hampe 2004) and genetic structure (Kudoh & Whigham 1997; Lundqvist & Andersson 2001; DeWoody *et al.* 2004) of riparian plant communities. We are, however, not aware of any published experimental tests of the relative importance of hydrochory for plant colonization and subsequent species richness in vegetation.

Large numbers of plant propagules are transported by rivers and deposited in riparian zones (Nilsson & Grelsson 1990; Boedeltje *et al.* 2003; Goodson *et al.* 2003), but the degree to which plants from these propagules establish there is poorly known (Andersson & Nilsson 2002). Levine (2003) modelled the role of

hydrochory for streamside vegetation, and found that, with realistic seed dispersal patterns and a uniform distribution of parent plants, most seed input to a riparian site would come from nearby patches upstream. Downstream dispersal of plants would increase population sizes and diversity only if populations are strongly seed limited (Levine 2003).

To resolve the conflict in expectations between theory and empiricism, we tested the role of hydrochory for plant colonization in riparian zones in a field study in two adjacent rivers, one free-flowing and the other regulated by dams. In large boreal rivers, most propagules are dispersed during the spring flood, which is also a major disturbance event redistributing sediment and organic matter, removing plants and creating space for colonization (Malanson 1993; Naiman & Décamps 1997; Jäkäläniemi *et al.* 2005). Our first hypothesis is that if hydrochory is important for plant colonization, more species per year should arrive and establish in plots open to floods and deposition of water-dispersed propagules than in unflooded control plots (excluding plants growing vegetatively into the plots by suckers, rhizomes or stolons). If this is not true, we can assume that the two types of plots share a common propagule source consisting of local plants that are dispersed by means other than water.

We also investigate the effect of hydrochory on species richness: it may increase the pool of colonizing species by facilitating long-distance dispersal, resulting in more species-rich plant communities, or may only increase the abundance of species already present in the local seed rain, having little effect on species composition. However, increased numbers of colonists may increase inter- and intraspecific competition and influence composition through differential survivorship. We further predicted that the flora of water-dispersed propagules should be more similar in composition to the flora of flooded than unflooded plots, that plots subject to flood disturbance and deposition of hydrochore should develop more species-rich plant communities with time (i.e. after several seasons of succession) than unflooded ones, despite any plant mortality caused by floods, and that fragmentation by dams should reduce the diversity and abundance of water-dispersed propagules, as dams block dispersal by water (Andersson *et al.* 2000a). Finally, given that daily and weekly water-level fluctuations, combined with ice-scour, result in high plant mortality along run-of-river impoundments in northern Sweden (Jansson *et al.* 2000a), such sites may have more recruitment-limited riparian plant communities, for which hydrochory is an important determinant of species composition.

Materials and methods

STUDY AREAS

The study was conducted along the Ume and Vindel Rivers in northern Sweden in the boreal coniferous

zone, in a cold-temperate climate (Walter 1985). The rivers are approximately equal in size and run parallel to each other in the same catchment. Both are seventh-order rivers, forming an eighth-order river as they join about 30 km upstream from the Gulf of Bothnia. The Vindel River is free flowing and exhibits seasonal water-level fluctuations ranging up to 6 m in height. Annual peak discharge occurs in June, after which mean water levels recede gradually, except for a minor, rain-induced increase in the autumn. Run-of-river impoundments have been constructed along the middle and lower main channel of the Ume River to provide water to hydropower stations. Throughout the year, water levels fluctuate daily or weekly between statutory high and low levels (in most cases 0.5–1 m apart). The Vindel River margins experience wave erosion (along wide reaches), shear forces from flowing water and ice scour. The Ume River margins lack most of the disturbance associated with flowing water, but experience strong disturbance due to frequent water-level fluctuations, wave erosion and severe ice-scour during winters. The river-margin vegetation along the Vindel River is distinctly vertically zoned, from riparian forest communities furthest from the river, where total species richness peaks (Nilsson 1983), to shrub vegetation of predominantly *Salix* spp., to herbaceous communities dominated by graminoids nearer the active channel. Vegetation in the impoundments along the Ume River generally lacks such a distinct zonation and can be separated into a narrow strip without clear dominants close to the high-water level above a zone with sparse cover of amphibious species.

STUDY DESIGN

To maximize realism of the study, we did not separate the associated effects of hydrochory and flooding, nor did we manipulate seed deposition. We created pairs of close-lying plots differing in elevation, one subject to flooding (i.e. affected by the input of water-dispersed seeds and flood disturbance) and another unflooded, serving as control. As adjacent plots were close enough to be in the same vegetation belt, and were surrounded by similar vegetation, we assumed that the seed rain would be similar between the plots, except for the input of hydrochorous seeds into flooded plots. This allowed us to estimate numbers of individuals and species of propagules per area of riparian ground with and without hydrochory and flood disturbance.

In the Vindel River we selected a 500-m long reach with silty riparian soils, spanning the transition zone from turbulent to tranquil flow. The reach was situated 167 m above sea level, 74 km from the confluence with the Ume River. We divided the reach into 20 sections, and established plots, 50 × 50 cm in size, at seven different elevations in the middle of 18 of these sections. The vertical distance between adjacent plots was 50 cm, which means that the total range in elevation was 300 cm, going from the transition between the

shrub and the riparian forest zone (flooded at least once a year) up into rarely flooded upland vegetation. This enabled adjacent pairs of flooded and unflooded plots to be selected, depending on the current year's flood level. In the Ume River we selected two 250 m long reaches, situated 3.5 km from each other in the same run-of-river impoundment, 222 m above sea level and 114 km from the confluence with the Vindel River. Each reach was divided into 10 sections. In the centre of each section we placed two 50 × 50 cm plots, one immediately below and another above the high-water level. The difference in elevation between the upper and lower plots was 30 cm at the upstream and 10 cm at the downstream reach. Adjacent plots, separated by 10–50 cm in elevation depending on site, were surrounded by similar plant species, making the assumption of similar local seed rain realistic. To standardize soil between plots, and to remove the seed bank, we replaced the original soil in plots along both rivers with a minimum of 25 L of a mixture of silt and compost (85% vs. 15%) to a depth of at least 10 cm. Seeds are unlikely to emerge from depths greater than this, but shoots from rhizomes and suckers emerged in a few cases.

The plots were established in September and October 1996 and monitored from 1997 to 1999. In 1997 we mapped all vascular plant individuals once every 2 weeks, starting in early July and ending in September (five visits). In 1998 and 1999 we made one visit in late August, mapping all plants. We noted whether individuals had originated from dispersed propagules (seeds or vegetative) or had grown vegetatively into the plot by suckers, rhizomes or stolons. We also noted whether or not the plot had been flooded (based on deposits of river-transported organic matter and gauging records), the volumetric proportion of soil loss (estimated by eye), and the percentage cover of bryophytes and leaf litter. We recorded all species present in the riparian zones of the entire reaches.

In early July 1997, we sampled litter deposited by the river to estimate the abundance and species composition of waterborne propagules. We divided the central 10 m of each section into 1-m subsections and collected all deposits of riverborne organic matter (drift), excluding woody debris, from a 20 × 30 cm area in the subsection with most drift. Drift is deposited in packs along the high-water level, ensuring that fine material, including seeds, can be sampled. We applied half of a 1-L sample from each drift collection to each of two 0.25 m² common garden plots and monitored them for seedling emergence. Plots were regularly irrigated and individuals were removed after identification. The pre-existing seed bank in the garden plots was evaluated using control plots without drift application, and emerging species were removed from analysis. To estimate the composition of the soil seed bank in natural soils at the sites, we took eight soil cores (2.2 cm in diameter and 10 cm deep) at each riverbank plot in 1997, 5 cm from the plot edge. The soil cores from each

plot were mixed and sown onto common garden plots as for the drift samples, and monitored for seedling emergence.

DATA ANALYSES

We classified the species according to *morphology* into woody, herb or graminoid species, and according to *habitat affinity* into riparian + terrestrial vs. aquatic species (following Nilsson 1983). We also classified species according to whether or not they had adaptations to dispersal by wind, vertebrates, vegetative dispersal or if they lacked specific adaptations for dispersal, following Johansson *et al.* (1996). As a measure of floating capacity, we classified species with seeds and fruits that float for 2 days or more as long-floaters and the remainder as short-floaters (Romell 1938; Danvind & Nilsson 1997; Andersson *et al.* 2000b). When several times were available for a species, we used the mean floating time. However, most data come from Romell (1938), in which the longest floating time is reported in classes, often as a range (e.g. days to months), and we consistently used the average of this range. All classifications included the entire flora, except for floating capacity, for which data were available for only 49 of 63 taxa (excluding taxa not identified to species).

To minimize differences between plots unrelated to flooding, we always compared only the plots immediately above and below the maximum water level for the present year (separated by 10–50 cm in elevation depending on site). We combined the data from the two reaches along the Ume River in the analyses, because variation among plots exceeded variation among reaches. We used SPSS version 11.0 (SPSS Inc., Chicago, Illinois, USA) for the statistical analyses, with a few exceptions indicated below.

To test whether hydrochory increased the number of colonizing species per plot, we used repeated measures ANOVA, testing for differences between flooded and unflooded plots and between years of inventory (1997–99). We tested for differences in the number of species per plot, the number of colonizing individuals and the mortality rate of individuals (all species combined) per plot, only counting individuals derived from seeds or vegetative propagules (i.e. excluding plants growing into the plots by suckers, rhizomes or stolons). We also tested for differences in the percentage cover of leaf litter and bryophytes, and the proportion of soil loss per plot. In the free-flowing Vindel River, the same sets of plots were flooded in 1997 and 1998 (with one exception), allowing for comparisons between these years. As the spring flood of 1999 was lower in magnitude, we analysed the 1999 data from the Vindel River separately using one-way ANOVA with flooding treatment as a fixed factor. In the Ume River, the same sets of plots were flooded each year, allowing comparisons between all 3 years of inventory. We also tested for correlations between plant colonization variables (number of colonizing individuals and species, as well as mortality

per plot) and the environmental variables measured (cover of leaf litter and bryophytes, and proportional soil loss), controlling for whether or not a plot had been flooded (partial Pearson product-moment correlations). Although pairs of flooded and non-flooded plots had the same soil and were surrounded by similar vegetation, they might have differed in factors unrelated to flooding because they were situated at different elevations. As we had plots on seven elevations in the Vindel River, we tested for a relationship between the number of colonizing species per plot and elevation on the riverbank, after accounting for the variability of flooding, using partial correlation.

To test whether hydrochory increased the pool of colonizing species, we constructed species accumulation curves by combining data from increasing numbers of plots in random order repeated 50 times, using the statistical software EstimateS (Colwell 2004). We tested whether species with certain traits were over-represented among the species unique to flooded plots compared with the total pool of colonizing species in each river, using χ^2 tests. We tested for differences in the proportion of species using all four classifications (habitat affinity, morphology, dispersal and floating time).

We calculated similarity in species composition between drift samples and plots for each section using Simpson's index of similarity (number of matches divided by the number of species in the sample with fewer species), and tested the hypothesis that mean similarities should be higher when drift samples were compared with flooded rather than unflooded plots, using paired samples *t*-tests. To test whether flood disturbance resulted in more species-rich plots, we compared species richness per plot depending on year of inventory and flooding conditions using repeated measures ANOVA.

To test whether the diversity of hydrochores is lower in a river fragmented by dams, we compared the volume of river-transported drift and the number of individuals and species of emerging seedlings per litre of drift between rivers using *t*-tests. We also estimated the number of emerging seedlings per 20 × 30 cm sampled drift patch by multiplying the number of emerging seedlings per litre of drift by the sampled volume. We estimated species richness of the viable propagule flora per litre of drift. To obtain an area-based measure of drift species richness we calculated a range of species richness estimators that predict the 'asymptotic' species richness by extrapolation, as differences in species abundance would have made a simple multiplication of species per litre of drift by area erroneous. We used several estimators as they differ in bias and precision (Brose *et al.* 2003): the incidence-based coverage (ICE), the first- and second-order Jackknife (Jackknife 1 and 2), the Chao 2, and Bootstrap richness estimators, and the Michaelis-Menten mean species accumulation function, using EstimateS software package, version 7.0 (Colwell 2004).

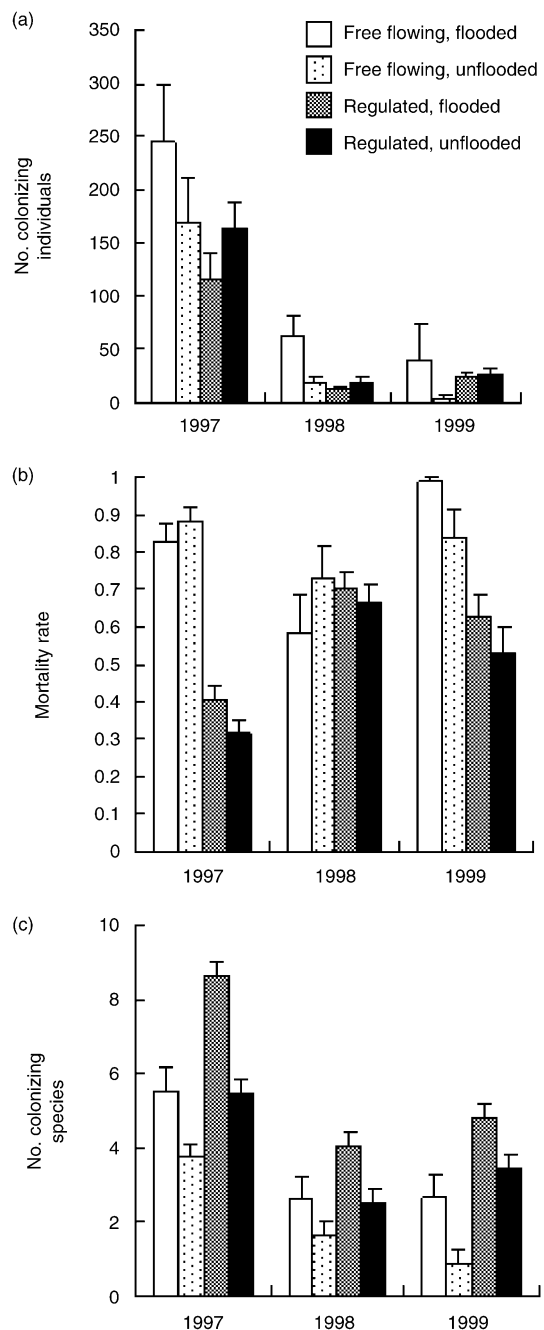


Fig. 1 Comparison of (a) mean number of colonizing individuals, (b) mean mortality rate and (c) mean number of colonizing species per plot between flooded and unflooded plots in the free-flowing Vindel and regulated Ume Rivers in the years 1997–99. Only individuals derived from seeds or vegetative propagules were counted.

Results

The number of colonizing species was 40–200% higher (corresponding to one to three species) on flooded compared with unflooded plots (depending on year and river), and higher in 1997 than in the following years (Fig. 1, $P < 0.05$, repeated measures ANOVA). When controlling for whether or not a plot was flooded, we found no significant correlation between number of colonizing species and elevation on the

Table 1 Results of repeated measures ANOVA comparing the number of colonizing individuals, mortality rate and number of colonizing species among years (1997 and 1998 in the Vindel River, 1997–99 in the Ume River) and between plots differing in flooding conditions (flooded vs. unflooded pairs of plots). Significant *P*-values ($P < 0.05$) are in bold

Source of variation	Vindel River				Ume River			
	d.f.	MS	<i>F</i>	<i>P</i>	d.f.	MS	<i>F</i>	<i>P</i>
Number of individuals								
Within subjects								
Year	1	80.3	57.0	< 0.0001	2	55.4	54.1	< 0.0001
Year × Flooding	1	0.6	0.4	0.51	2	1.2	1.1	0.33
Error	31	1.4			72	1.0		
Between subjects								
Flooding	1	1.9	0.7	0.41	1	0.7	0.7	0.41
Error	31	2.7			36	1.0		
Mortality rate								
Within subjects								
Year	1	0.40	4.4	0.046	2	1.0	22.8	< 0.0001
Year × Flooding	1	0.07	0.8	0.39	2	0.001	0.2	0.79
Error	30	0.09			72	0.004		
Between subjects								
Flooding	1	0.07	2.9	0.10	1	0.15	2.0	0.17
Error	30	0.07			36	0.008		
Number of species								
Within subjects*								
Year	1	108.8	57.7	< 0.0001	1.4	225.3	54.5	< 0.0001
Year × Flooding	1	2.9	1.5	0.23	1.4	15.1	3.7	0.047
Error	32	1.9			51.7	4.1		
Between subjects								
Flooding	1	31.1	7.4	0.011	1	124.2	11.5	0.002
Error	32	4.2			36	10.8		

*The Greenhouse-Geisser Epsilon adjustment was made because the sphericity assumption was violated.

riverbank in the Vindel River ($r = 0.09$, $P = 0.11$, $n = 321$, partial correlation). We found no significant difference in the number of colonizing individuals between flooded and unflooded plots in either river ($P > 0.05$, repeated measures ANOVA, Fig. 1, Table 1).

In both rivers, the number of colonizers was higher in 1997 than in the following years ($P < 0.05$, repeated measures ANOVA, Table 1), but this year was also more intensively sampled. The mean mortality rate of colonizing individuals did not differ significantly between flooded and unflooded plots ($P > 0.05$, repeated measures ANOVA, Table 1), except for 1999 in the Vindel River, when mortality was higher on flooded than on unflooded plots ($P = 0.044$, one-way ANOVA). The mean mortality rate per plot differed among years, but the temporal pattern was different in the two rivers (Vindel lowest in 1998, Ume lowest in 1997, Fig. 1).

The pool of colonizing species was larger on flooded than unflooded plots at all spatial scales created by incrementally combining the flora from increasing numbers of plots (Fig. 2). The cumulative species richness of all plots combined was 40–56% higher on the flooded than the unflooded plots in the Vindel River, and 36–58% higher in flooded plots in the Ume River, depending on year. We analysed the entire assemblage of species that colonized flooded vs. unflooded plots by combining the 1997 and 1998 data because the same plots were flooded in both years. In the free-flowing

Vindel River, 40 species colonized the flooded plots compared with 20 species on the unflooded plots. Fifty-six species colonized the flooded plots in the regulated Ume River, compared with 31 species on the unflooded plots. Two species were unique to the unflooded plots in the Vindel River, and six species, all of which were rare and represented by up to five occurrences, were unique to unflooded plots in the Ume River. All colonizing species were found in the established riparian vegetation along the local reach except *Crassula aquatica*, which colonized a flooded plot in the Ume River.

Twenty-two and 19 species were unique to flooded plots in the Vindel and Ume Rivers, respectively. In both rivers, aquatic and herbaceous species, as well as species without specific adaptations for dispersal, were over-represented among the species unique to flooded plots ($P < 0.05$, χ^2 tests, Appendix S1 in Supplementary Material). In flooded plots, aquatic species were 79 and 80% more frequent than expected due to chance on the Vindel and Ume Rivers, respectively. Herbaceous species were 37% and 45% more frequent, and species lacking specific adaptations for dispersal 43% and 31% more frequent, in flooded than in unflooded plots. In addition, species with adaptations for vegetative dispersal were 53% more frequent than expected among those unique to flooded plots in the regulated river ($P < 0.004$, χ^2 test). We found no significant difference in the proportion of species with different propagule

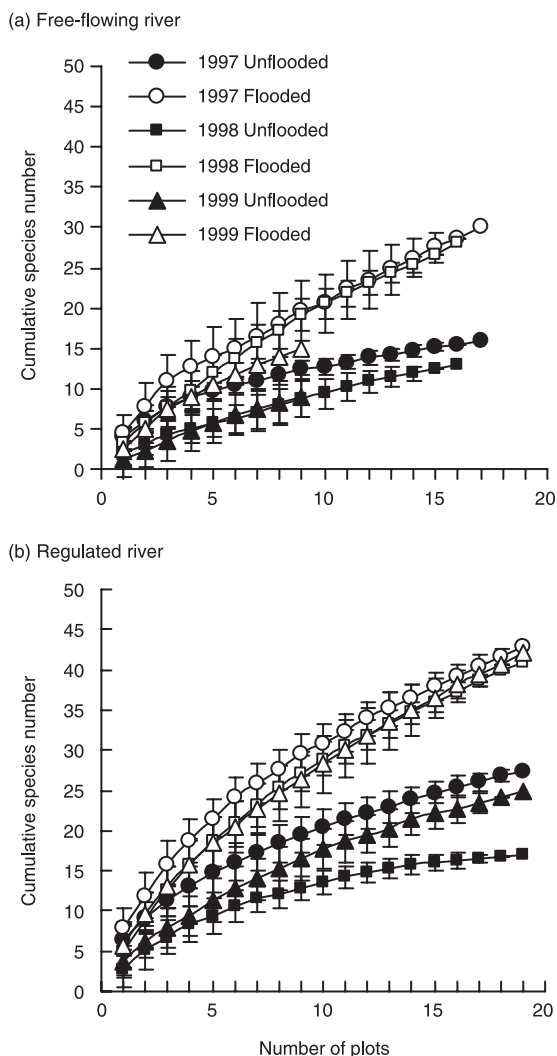


Fig. 2 Species accumulation curves for species derived from seeds or vegetative propagules (excluding plants growing vegetatively into the plots by suckers, rhizomes or stolons) colonizing flooded and unflooded plots in (a) the free-flowing Vindel River and (b) the regulated Ume River in 3 years (1997–99). The species accumulation curves were constructed by combining data from increasing numbers of plots in random order. This was repeated 50 times to obtain mean values and standard deviations of species richness for each number of plots, using the statistical software EstimateS (Colwell 2004). The low number of plots in the Vindel River in 1999 is because a spring flood of low magnitude left many sections unflooded, and these were excluded from analysis.

floating abilities between flooded and unflooded plots in either river ($P = 0.71$, χ^2 tests). Many of the species that were abundant in the drift samples were also among the most common colonizers of flooded plots in both rivers. Some of these, such as *Betula pubescens* and *Filipendula ulmaria*, are naturally abundant in the riparian forest zone where most of our plots were situated. In contrast, other species in drift, such as *Carex acuta*, *Potentilla palustris* and *Ranunculus repens*, are more abundant in natural vegetation at lower elevations. Thus, hydrochory displaced the propagules of these species from lower elevations but, over time, they

are likely to be competitively inferior to species growing naturally at higher elevations.

The mean similarity (Simpson's index) between the floras in drift and in flooded plots was higher than for the comparison between drift and unflooded plots in the Ume River [0.35 ± 0.049 vs. 0.25 ± 0.054 (mean \pm SE), 20 riverbank sections, $P < 0.05$, one-tailed Wilcoxon signed ranks test]. In contrast, the floristic similarity was higher between drift and colonists of unflooded plots than for flooded plots in the Vindel River (0.47 ± 0.066 vs. 0.19 ± 0.054 , $n = 15$, $P < 0.01$, Wilcoxon signed ranks test). Although there were more species on the flooded than on the unflooded plots in the Vindel River, the number of species shared with the drift flora did not differ between flooded and unflooded plots ($P > 0.05$, Wilcoxon signed ranks test), i.e. the extra species that colonized the flooded plots were not found in the drift samples. When comparing the pooled species lists of the drift and plots with different flooding conditions, the similarity (Simpson's index) was 0.55 for flooded and 0.36 for unflooded plots in the Ume River, compared with 0.49 and 0.47 for the Vindel River. Few species emerged from the soil seed bank samples, and the data were not analysed further.

Plots subject to flood disturbance and deposition of hydrochores developed more species-rich plant communities than unflooded ones in both rivers. The mean number of species per plot derived from propagules (both colonizing and surviving from previous years) was higher on flooded plots in both rivers ($P < 0.05$), whereas we found no significant difference in numbers of vegetative species between flooding treatments (Fig. 3, $P > 0.05$, repeated measures ANOVA). The number of propagule-derived species in the Vindel River decreased as a function of time ($P < 0.05$), but vegetative species richness did not differ between years (Fig. 3a, $P > 0.05$, repeated measures ANOVA). We found no significant difference in numbers of species of any origin (propagules or vegetative) among years in the Ume River (Fig. 3b, $P > 0.05$, repeated measures ANOVA). The cumulative richness of all surviving species in all plots combined was 25–76% higher on flooded compared with unflooded plots depending on river and year.

The volume of deposits of riverborne organic matter (drift) per section was larger and the number of emerging seedlings per litre of drift was five times higher in the Vindel than in the Ume River (Table 2). When we removed the most abundant species, *Carex acuta*, the relationship was reversed, with twice as many seedlings in the Ume River (Table 2). The estimated number of emerging seedlings per riverbank patch (i.e. drift volume per 20×30 cm large patch multiplied by number of seedlings per litre of drift) was nine times higher in the Vindel than the Ume River but, with *Carex acuta* excluded, the difference was not significant (Table 2). The number of emerging species per litre of drift was significantly higher in the Ume River (Table 2).

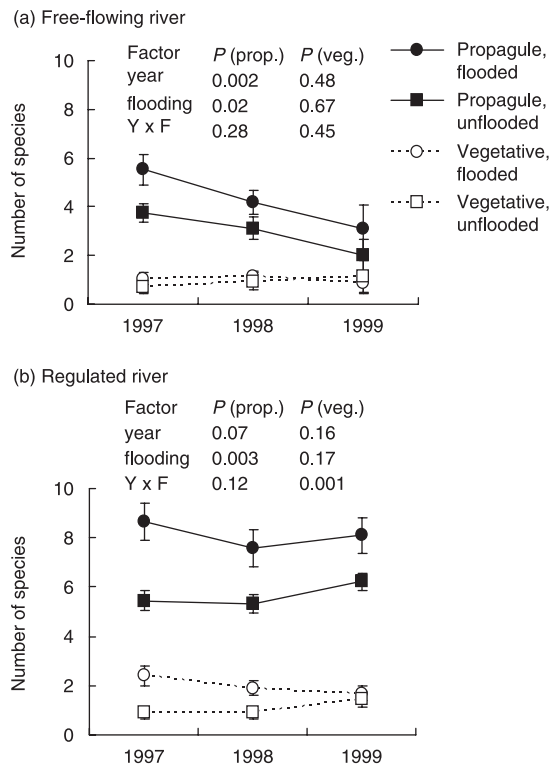


Fig. 3 Total number of species present per plot, either colonizing during the present year or surviving from previous years, in flooded (circles) vs. unflooded (squares) plots from (a) the free-flowing Vindel River and (b) the regulated Ume River. Species may be derived from propagules (closed markers and solid lines) or grow vegetatively into the plots by suckers, rhizomes or stolons (open markers and dashed lines).

Estimates of the number of emerging species in the drift obtained by extrapolation were very similar between the rivers, differing by only one or two species depending on the richness estimator used (Table 2). Species found in the drift flora were present in the established riparian

vegetation of the local reach, with the exception of *Angelica archangelica* in the drift from the Vindel River, and *Menyanthes trifoliata* and *Peucedanum palustre* in both rivers.

In the Vindel River, leaf litter cover was negatively correlated with the number of colonizing individuals ($r = -0.71$, $P < 0.0001$, 319 observations) and species ($r = -0.45$, $P < 0.0001$, 318 observations, partial correlations controlling for flooding treatment), but correlations between numbers of species or mortality and the other environmental variables were not significant ($P > 0.05$). In the Ume River, leaf litter cover was negatively correlated with number of colonizing individuals ($r = -0.44$, $P < 0.0001$, 90 observations) and species ($r = -0.35$, $P = 0.001$, 90 observations), and positively correlated with mortality ($r = 0.45$, $P < 0.0001$, 90 observations). In addition, number of colonizing individuals was negatively correlated with bryophyte cover ($r = -0.29$, $P = 0.002$, 110 observations). Neither leaf litter nor bryophyte cover differed significantly between flooded and unflooded plots in either river ($P > 0.05$), but soil loss was higher from flooded plots in both rivers ($P < 0.05$, repeated measures ANOVA, Appendices S2 and S3). However, soil loss almost exclusively occurred in 1997 before the plots were monitored (Appendix S2).

Discussion

The study supports the hypothesis that hydrochory is important for plant colonization and enhancement of species richness in riparian plant communities. A major advantage with the design comparing pairs of close-lying flooded and unflooded plots was that patterns of seed deposition were not manipulated, and the experimental treatments comprised combinations of naturally occurring (rather than imposed) dispersal processes. Integrating the effects of hydrochory and

Table 2 Comparison of drift volume and drift flora characteristics between the free-flowing Vindel River and the regulated Ume River. Significant *P*-values ($P < 0.05$) are in bold

	Vindel River 16 samples (Mean \pm 1 SE)	Ume River 20 samples (Mean \pm 1 SE)	<i>P</i> *
Drift volume per patch (L)	8.1 \pm 1.02	4.5 \pm 0.66	0.004
Number of emerging seedlings/L of drift	389 \pm 99.6	78 \pm 7.6	0.001
Ditto excluding <i>Carex acuta</i>	36 \pm 4.6	73 \pm 7.6	< 0.0001
Number of emerging seedlings/patch	3040 \pm 821.3	328 \pm 40.4	0.001
Ditto excluding <i>C. acuta</i>	337 \pm 66.1	301 \pm 37.5	0.62
Number of emerging species/L of drift	12.1 \pm 0.88	15.4 \pm 0.86	0.013
Extrapolated drift species richness†			
ICE	106	104 \pm 4.5	
Jackknife 1	94 \pm 5.0	93 \pm 5.1	
Jackknife 2	108	107 \pm 4.1	
Chao 2	97 \pm 15.6	99 \pm 17.7	
Bootstrap	79	78 \pm 1.4	
Michaelis-Menten mean	77	76	

*Probability of no difference (*t*-tests, two-tailed probability).

†Estimated species richness according to non-parametric estimators and a species accumulation function finding the asymptotic species richness (the Michaelis-Menten mean model).

flood disturbance added realism because waterborne propagules generally are deposited during floods. However, the species richness of colonizing plants could be higher on the flooded plots for reasons unrelated to hydrochory. For instance, although soil and species composition of the surrounding vegetation were similar within pairs of plots, soil moisture might have been higher on the lower, inundated plots, which could benefit seedlings sensitive to desiccation. However, the number of colonizing individuals per plot did not differ between adjacent flooded and unflooded plots (Fig. 1), indicating that conditions for germination were similar, or that differences in soil moisture were of significance only to rare species. We found no significant correlation between number of colonizing species and elevation on the riverbank, when the effect of flooding was controlled for, indicating that flooding was more important than elevation in determining diversity of colonizers. Soil moisture increases linearly towards lower elevations (R. Jansson, unpublished observations), and a positive correlation would have been expected if soil moisture *per se*, rather than flooding, was important for numbers of colonizing species. The fact that almost all species encountered on the unflooded plots were also found on the flooded ones further implies that conditions for germination and dispersal vectors other than hydrochory did not differ in any significant way. The few species that were found exclusively on unflooded plots were all rare, and these occurrences could equally be the result of chance as of sensitivity to flooding, although they included known sensitive species, such as *Vaccinium myrtillus*.

A final concern would be if flooding increased the heterogeneity of the flooded plots, providing suitable conditions for more species. Such heterogeneity would not be related to soil conditions, as soils were the same among plots, and we found no significant difference in cover of litter and bryophytes between treatments in either river (Appendix S2). In fact, flooding is likely to increase the homogeneity of the plots once water has receded. No sediment deposition was observed on the plots. Furthermore, plant cover was low in all plots (< 25%), making it unlikely that competitive interactions affected patterns of colonization or species richness in plots. Given that these alternative explanations have little support, we conclude that the differences in numbers of colonizing species are best explained as an effect of hydrochory.

If hydrochory resulted in the introduction of more species to flooded plots, a logical question is: What was the effect of flood disturbance on plant colonization? A major effect of floods is to remove plants and open up patches for colonization in riparian zones (Naiman & Décamps 1997; Pollock *et al.* 1998; Bendix 1999). We manipulated soil conditions to create open patches, making this effect of flooding irrelevant for the results. Flooding may also cause plant mortality by drowning (Blom & Voeselek 1996; Johansson & Nilsson 2002) and sediment and litter deposition (Xiong & Nilsson

1997). Mortality of colonizers did not differ between flooded and unflooded plots except for 1999 in the Vindel River. In the Ume River, ice disturbance can be severe, explaining the higher mortality in 1998 and 1999 (following winters) than during the growing season of 1997, when the plants were first recorded. In the Vindel River, many seedlings were killed by drought in 1997 and by leaf litter accumulation in 1999, and mortality was lowest in 1998 (Fig. 1). Soil was eroded from some of the flooded plots, but primarily during the spring flood of 1997 before the plots were monitored, and the mortality caused by this disturbance was unrecorded. In conclusion, despite any negative effects of flood disturbance on plant establishment, flooding resulted in more species successfully colonizing riparian sites.

The fact that the difference in cumulative species richness between flooded and unflooded plots (Fig. 2) was as large as differences between individual plots for the two environments supports the hypothesis that hydrochory increased the pool of colonizing species, and suggests that hydrochory is also important for the diversity of colonizing species at the reach scale (i.e. combinations of many open patches distributed over a large area). The fact that only one colonizing species was absent from the local riparian vegetation might be interpreted either as showing that hydrochory is effective and most species are therefore expected to be present in suitable riparian habitats, provided that seed production is not limiting, or that within-reach dispersal predominated. The Vindel River has a large potential for long-distance dispersal by water; in an experiment with floating seed mimics, the average dispersal distance in the vicinity of the experimental reach was 40.3 km, and the longest recorded dispersal distance was 152.5 km (Andersson *et al.* 2000b). In contrast, the sites in the Ume River were situated 1.6 and 5.0 km below a dam across which dispersal is unlikely, and were colonized by as many species as the Vindel River site. To resolve the issue of the relative importance of long-distance dispersal for plant colonization, further studies need to focus on dispersal distances, using molecular markers of genetic structure, or monitoring the longevity and reach-scale turnover of plant populations.

The flooded plots were colonized by many species that were absent in the unflooded plots. These species often had adaptations expected for waterborne seed dispersers: flooded plots included more aquatic and herb species as well as species without specific morphological adaptations for dispersal, and (in the Ume River) vegetatively dispersed species. Species lacking dispersal adaptations may still float well in water, as do most vegetative propagules. However, long-floating species were not over-represented among the species colonizing flooded plots in either river. In contrast, Johansson *et al.* (1996) found a positive correlation between the floating time of propagules and the frequency of species in the riverbank flora. Previous studies have also found an over-representation of

long-floating species in riparian zones along tranquil reaches (Jansson *et al.* 2000b; Nilsson *et al.* 2002). In these studies, it was suggested that the prevalence of long-floating species results from filtering of short-floating propagules, which may sink before they can be washed ashore and deposited in a riparian zone. According to our results, such filtering was not strong enough to make long-floating species significantly more effective than short-floating ones in colonizing riparian zones.

The higher similarity between the propagule flora in the riverborne drift and the flooded plots than between the drift and the unflooded plots in the Ume River corroborates the view that the higher diversity could be attributed to deposition of water-dispersed propagules, but the opposite pattern was found in the Vindel River. In free-flowing boreal rivers, water-dispersed seeds are generally deposited in the riparian forest zone only once a year during the spring flood. In contrast, in run-of-river impoundments, the riparian zones are flooded and drained weekly or even daily, enabling deposition and erosion of propagules throughout the growing season. This difference in flooding frequency may explain the different similarity patterns, or the seeds of some species in drift deposits in the Vindel River may have lost their viability by the time the samples were taken, or seedlings may have germinated and died.

The hypothesis that flooded plots developed more species-rich plant communities was also supported (Fig. 3), indicating that the positive effect of colonization by hydrochory outweighed any negative effects of mortality due to flood disturbance. However, the plots were only evaluated for 3 years, and long-term trajectories of plant community development are unknown.

Although there were large differences in water-level regime, the results of the experiment were highly similar between rivers, indicating that hydrochory may be important in regulated rivers. Despite the fact that dispersal across dams is unlikely (Andersson *et al.* 2000b), the species richness of the drift flora in the Ume River was higher, and the estimated asymptotic species richness was similar to the Vindel River (Table 2), providing little support for the hypothesis that fragmentation by dams reduced the diversity and abundance of water-dispersed propagules. The drift flora in the Ume River probably relied on local (within-impoundment) propagule sources. The extrapolated estimates of drift species richness were almost an order of magnitude larger than the number of species per litre of drift. This was because many species in the drift were rare, resulting in high turnover between drift samples. Differences in species richness between flooded and unflooded plots were similar in magnitude between rivers, both for mean values per plot and cumulative values. Jansson *et al.* (2000b) found that riparian floras differed among pairs of otherwise similar run-of-river impoundments separated by dams, and interpreted this as the result of dams acting as barriers to dispersal. Effective plant dispersal by water among spatially separated riparian

populations within impoundments would homogenize species composition among sites, potentially accentuating differences between impoundments. As most plant populations are smaller and likely to have higher turnover in run-of-river impoundments than in free-flowing rivers (Jansson *et al.* 2000a), hydrochory might be more important for species composition in regulated rivers, although dispersal is probably only local (within impoundments) except in years with exceptionally high run-off, when dam spillways are used.

It is clear from these findings that hydrochory is important for the colonization of new riparian sites in free-flowing as well as in regulated rivers, and that the positive effect on both numbers of colonizing species and standing species richness remains when spatial scale is increased to that of riparian reaches. The high diversity of riparian zones has generally been attributed to intermediate levels of disturbance from floods, reducing dominance and allowing competitively inferior species to persist. This study implies that hydrochory may also be an important factor for riparian species richness. The significance of hydrochory may lie in the form of the dispersal curve: whereas most dispersal vectors exhibit exponential decay in the number of propagules per distance (Willson 1993), buoyant propagules may be dispersed long distances in flowing water, irrespective of their mass. Thus, riparian plant communities may receive a comparatively large proportion of their seed rain by long-distance dispersal. A challenge for future studies will be to compare our results with field manipulations in other ecosystems, and to elucidate the degree to which other types of communities are structured by dispersal.

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Supplementary material

The following supplementary material for this paper is available from <http://www.Blackwell-Synergy.com>:

Appendix S1 Table showing the results of χ^2 tests of the proportion of species with different traits compared between species that were unique to the flooded plots and the total pool of species colonizing by propagules.

Appendix S2 Table showing mean values and standard errors for environmental variables recorded per plot and year of inventory compared between flooded and unflooded plots.

Appendix S3 Table showing the results of ANOVAs comparing environmental variables among years and between flooding treatments.