

Short Communication

EFFECTS OF RIVER FRAGMENTATION ON PLANT DISPERSAL AND RIPARIAN FLORA

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ABSTRACT

We evaluated the effects of river fragmentation by dams on hydrochory (i.e. plant dispersal by water) and on plant distribution by comparing two adjacent rivers in northern Sweden, one free-flowing and the other regulated. We collected stranded drift material from both rivers in order to quantify the drift material and its species content. We also estimated the floristic continuity along the two rivers by comparing the drift flora with the riparian flora further upstream. The drift amount deposited on the riverbank, its species richness and its contribution to the species pool were higher in the free-flowing than in the regulated river. The floristic continuity was also higher in the free-flowing than in the regulated river. Copyright © 2000 John Wiley & Sons, Ltd.

KEY WORDS: corridor fragmentation; hydrochory; plant dispersal; riparian vegetation; rivers; vascular plants

INTRODUCTION

Rivers are important pathways for the flow of energy, matter and organisms through the landscape (Forman and Godron, 1986; Malanson, 1993). Among organisms, rivers are used by migrating fish (Mills, 1971), drifting invertebrates (Waters, 1972; Poff and Ward, 1991) and plants (Romell, 1938; van der Pijl, 1969). In fact, most plants in riparian corridors can be dispersed by water (Johansson *et al.*, 1996), although their floating capacities vary considerably. The dispersal power of water contributes to the fact that riparian corridors are usually rich in plant species, maintain a series of successional stages (Salo *et al.*, 1986; Kalliola and Puhakka, 1988; Naiman *et al.*, 1993), and are target areas for the invasion and the spread of weeds and exotic species (Panetta and Hopkins, 1991; Pyšek and Prach, 1993; Décamps and Tabacchi, 1994).

Nowadays, most rivers in the world are regulated and fragmented by dams and may, therefore, be less effective as corridors (Petts, 1984; Dynesius and Nilsson, 1994). Vegetation changes following hydrological alterations have been documented, both for vascular plants (Nilsson *et al.*, 1991a; Nilsson and Jansson, 1995; Toner and Keddy, 1997) and for bryophytes (Englund *et al.*, 1997), but there are few observations on how river fragmentation by dams affects plant dispersal.

This paper will focus on plants which have been transported by water and deposited on the riverbank, and will address two main questions: (i) Does the amount and species content of stranded drift material differ between free-flowing and fragmented rivers? (ii) Does river fragmentation affect the distribution of plants and diaspore drift along the river?

Study sites

The field work was carried out along the middle and lower reaches of the free-flowing Vindel River and the regulated Ume River (Figure 1). Both rivers rise in the mountain chain that forms the border between

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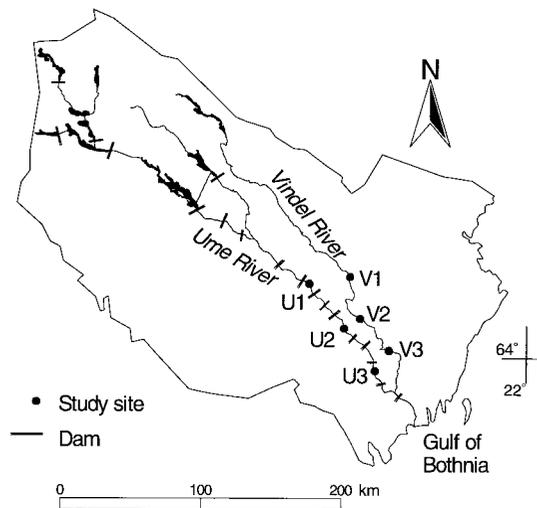


Figure 1. Location of the study sites. V1 = Forsholm, V2 = Bäckerforsen, V3 = Mittiforsen, U1 = Bålforsen, U2 = Johannelund, U3 = Fällforsen

Norway and Sweden, run parallel for 420 km, less than 56 km apart, and join 30 km above the Gulf of Bothnia, forming an eighth order river (Strahler, 1957).

The Vindel River exhibits large natural seasonal fluctuations in both water flow and water level. The discharge ranges between 15 and 1651 $\text{m}^3 \text{s}^{-1}$ at the confluence with the Ume River, with a mean of 174 $\text{m}^3 \text{s}^{-1}$ (The Swedish Meteorological and Hydrological Institute, 1979). During the growing season, the water level is at its highest in May–June and usually lowest in August–September. The river margin vegetation is distinctly zoned up the bank, going from forest communities at the top, to shrub vegetation in the middle, and to herbaceous communities at the bottom (Nilsson, 1983).

The Ume River was developed for hydroelectric power mainly during the 1950s and 1960s. It now consists of a stair-stepped series of storage reservoirs and run-of-river impoundments. In total, there are 20 major dams. The regulated discharge varies between 0 and 918 $\text{m}^3 \text{s}^{-1}$. The natural discharge varied between 40 and 1559 $\text{m}^3 \text{s}^{-1}$, with a mean of 240 $\text{m}^3 \text{s}^{-1}$ at the confluence with the Vindel River (The Swedish Meteorological and Hydrological Institute, 1979). Water levels usually fluctuate between 0.1 and 1 m in height either daily or weekly throughout the year in the studied run-of-river impoundments. In some storage reservoirs further upstream, however, seasonal water level fluctuations are larger, with a maximum range of 20 m. The river-margin vegetation is concentrated in a narrow strip close to the high-water level in the reservoirs and most impoundments.

METHODS

For the purposes of the study, we chose three sites, 45 km apart, in the middle and lower reaches of both the Vindel and the Ume Rivers (Figure 1). The three study sites in each river were situated at equivalent distances from the confluence of the two rivers. Each site consisted of a 200 m long section of riverbank, located on the northern riverside. We measured the height between spring high-water level and summer low-water level (riverbank height) in the free-flowing river, and the (equivalent) height between the highest and the lowest water levels in the run-of-river impoundments.

We divided the 200 m long sections into 20 subsections, each 10 m long. In each subsection, we measured the width of the entire riverbank and of the riparian forest and shrub zones, and counted the stems of trees and shrubs. We localized a 1 m^2 sample plot to the largest drift pile in each subsection. We noted the flora of vascular plant species, and estimated the percentage cover of field layer (dwarf-shrubs, herbs and graminoids), bottom layer (mosses and lichens), leaf-litter drift (needles, leaves and flower

parts) and wood-litter drift (dead stems, twigs and branches) in the plot. We then collected the leaf-litter drift—because leaf-litter mass has shown stronger correlations with plant community patterns than wood-litter mass (Nilsson *et al.*, 1991b)—and brought the samples to the laboratory, where they were dried at 60°C for 48 h, weighed and sifted. We then picked out 250 diaspores from each sample for identification, and calculated diaspore species richness as well as species proportions. This was carried out by spreading the sifted material over a flat surface and counting the diaspores up to 250 by moving a stick from one side of the scatter to the other. In a few samples with less than 250 diaspores, all were identified. This method produces radical measures, because species represented by dead diaspores will be added to the flora. An alternative method—to identify the flora through germination tests—is, however, unlikely to produce more significant results because of difficulties in providing the ideal germination requirements for all species.

We treated *Betula pubescens* + *B. pendula*, *Calamagrostis* spp., *Carex acuta* + *C. nigra*, *C. rostrata* + *C. vesicaria*, *Empetrum* spp., *Hieracium* spp., *Juncus* spp., *Luzula* spp., *Poa* spp., *Salix* spp., *Scirpus* spp., *Sparganium* spp., *Taraxacum* spp., *Thalictrum* spp., *Vaccinium* spp. and *Viola* spp. as one taxon each, hereafter referred to as 'species'. The nomenclature follows Mossberg *et al.* (1992). The field work was carried out at the end of June in 1992 (Vindel River) and 1993 (Ume River). This is justified by observational studies over the years suggesting that the variation in drift deposition among years does not exceed differences between the two types of rivers (Andersson, Nilsson and Johansson, unpublished data).

Data analysis

We tested the effects of fragmentation on the riparian vegetation and the dispersal of species along the river corridor by calculating the degree of floristic continuity for the two rivers. We compared the diaspore flora with the vascular plant flora at the particular sampling site and at ten upstream sites, 15 km apart. All sites comprised 200 m of the riparian corridor. For the upstream sites, we used vegetation data from Nilsson *et al.* (1991a) and compared the species pools of diaspores and vascular plants by calculating Sørensen's index of similarity (Kent and Coker, 1996): $2C/(n_1 + n_2 + 2C)$, where n_1 is the number of vascular plant species unique to the established vegetation, n_2 is the number of species represented only by diaspores in the drift deposits, and C is the number of common species, i.e. species found as both a plant and a diaspore. In an additional analysis, long-floating species (floating time ≥ 2 days) and short-floating species (floating time < 2 days) were treated separately. Buoyancy data for the different species were taken from Romell (1938), and Danvind and Nilsson (1997). In order to check for the potential contribution of diaspores from local plants, we also calculated the floristic similarity between the present vegetation and seed deposits for each 1 m² sample plot. We then tested for differences in floristic similarity between the rivers, in the number of species represented as diaspores, in the number of vascular plant species, and in the cover of deposited leaf-litter, using the Mann–Whitney U -test.

RESULTS

Free-flowing river

Drift deposits were present in 58 of 60 sample plots. The cover of stranded drift was not correlated ($p > 0.05$) with riverbank width, number of stems, or percentage cover of the field layer. At the upstream site, the total flora (vascular plants and diaspores) along a 200 m long section included 20 species (28%), which were represented only by diaspores; the middle site included ten such species (9%) and the downstream site 17 such species (19%). The mean proportion of long-floating species in the drift samples was 59% and of short-floating species was 8%; the remaining 33% are not yet tested for floating capacity.

Table I. Results from the comparison of the environmental variables, number of vascular plant species (200 m long stretches), and number of plants in the drift deposits (pooled for each set of 20 1 m² sample plots), between the two rivers (Mann–Whitney *U*-test, two-tailed test of probability, *n* = 3)

	Free-flowing	Regulated	<i>p</i>
Riverbank height (m)	2.3 ± 0.36	0.97 ± 0.56	<0.05
Riverbank width (m)	14.9 ± 4.6	4.5 ± 6.8	NS
Number of stems m ⁻²	2.4 ± 0.15	14.9 ± 12.7	NS
Plant cover (%)			
Bottom layer	11.5 ± 10.1	10.9 ± 5.4	NS
Field layer	17.6 ± 7.7	24.1 ± 13.2	NS
Drift cover (%)			
Leaf drift	37.0 ± 61	4.9 ± 4.1	<0.05
Wood drift	12.4 ± 6.4	0.9 ± 1.3	<0.05
Amount of drift (g m ⁻²)	242 ± 49.4	26 ± 21.7	<0.05
Number of diaspore species	40.3 ± 2.5	18.7 ± 7.0	<0.05
Number of species exclusive to the drift	16.0 ± 4.6	5.3 ± 3.2	<0.05
Number of vascular plant species	76.7 ± 27.1	66.0 ± 16.5	NS

The values are means and S.D.

Regulated river

Drift deposits were found in 23 of 60 sample plots. The cover of stranded drift was positively correlated with riverbank width and stem density ($p < 0.05$), and the number of species in the stranded drift increased with drift cover ($p < 0.01$). At the upstream site, nine species (12%) were represented only by diaspores. The corresponding figures for the middle and downstream sites were five (7%) and three species (4%), respectively. The mean proportion of long-floating species in the drift samples was 73%, and of short-floating species was 12%; the remaining 15% were not classified in terms of floating ability.

Floristic similarity

The total number of plant species in the drift and the cover of deposited drift were significantly higher in the free-flowing than in the regulated river ($p < 0.05$; Table I). The floristic similarity between the drift flora and the vegetation established at riparian sites further upstream was higher in the free-flowing river than in the fragmented river, both for the entire flora ($p < 0.05$) and for the long-floating species ($p < 0.05$; Table II). The similarity in species composition between the drift and the local vegetation was higher

Table II. Results from the comparison of floristic similarity between the drift flora on a study site and the vascular plant flora on ten sites upstream (regional similarity), and between the drift flora and the aboveground flora in the sample plots (local similarity) (Mann–Whitney *U*-test, two-tailed test of probability, *n* = 3)

	Free-flowing	Regulated	<i>p</i>
Regional similarity			
Entire flora	0.49 ± 0.02	0.37 ± 0.07	<0.05
Long-floating species	0.58 ± 0.01	0.46 ± 0.05	<0.05
Short-floating species	0.24 ± 0.13	0.19 ± 0.17	NS
Local similarity			
Entire flora	0.20 ± 0.03	0.11 ± 0.07	<0.05
Long-floating species	0.30 ± 0.02	0.28 ± 0.12	NS
Short-floating species	Too few data	Too few data	

The values are means and S.D.

along the free-flowing river than along the fragmented river ($p < 0.05$) for the entire flora, but there was no such difference for long-floating species ($p > 0.05$; Table II).

DISCUSSION

The floristic comparison of waterborne diaspore deposits with potential source communities further upstream in the rivers suggests that upstream–downstream similarities decrease after regulation. The probable mechanism for this is the restriction of hydrochory by dams. Nilsson and Jansson (1995) concluded that regulated rivers cannot create their own pattern of species richness by means of long-distance dispersal of plants, i.e. there is no regional regulation of the flora, but a dependence upon local contributions. Our comparison on the local scale (within sites), however, suggests that the floristic difference between waterborne plants and local vegetation has also increased after regulation. It could be that river regulation has not only reduced species richness in riparian habitats, but has also increased the heterogeneity of riparian vegetation, thus making it less likely that a set of diaspores waterborne over a short distance will be similar to the standing vegetation at the site where they are deposited. It could also be that outputs and inputs of local species do not match because diaspores sink during transport. The fact that the species composition did not vary between local vegetation and deposits of long-floaters supports the latter explanation. Long-floaters can stay afloat long enough to survive the time it may take them to finally be deposited on the riverbank along a run-of-river impoundment.

Many structures and functions of rivers are affected by dams and impoundments and this may contribute to changes in the redistribution of drift material, including diaspores. First, flood events are considered to be essential for the persistence of riverine systems (Pinay *et al.*, 1990; Naiman *et al.*, 1993). The absence of floods eliminates the lateral (riparian–aquatic) movement of drift material, both to and from the riverbank, as well as the transport of drift along the river (see Ward, 1989). Another notion is that the redistribution of sediment and organic debris is a key process of free-flowing riparian corridors (Ward, 1989; Malanson, 1993) which are obstructed along regulated rivers (Xiong and Nilsson, 1997). We found very small amounts of organic debris along the regulated river (Table I), and judging by the leaves included, most of it was of local origin. Furthermore, species represented only by diaspores were more numerous on the riverbank in the free-flowing river (9–28%) than in the regulated river (4–12%). Hughes and Cass (1997) documented similar values, that 14% of the species were represented only as diaspores in the flood debris along a fourth order free-flowing stream.

Second, riverbanks along lake-like impoundments are usually exposed to increased wave action because of channel widening, and frequent water-level fluctuations resulting from flow regulation in the power stations. These actions change the structure of the riverbank by eroding the fine-grained substrates, and in the winter an expanding ice sheet compresses the riverbanks making them even more erosive (Sundborg, 1977). These disturbances make plant establishment difficult. The positive relationships between the cover of drift material, riverbank width, and the number of tree and shrub stems in the sampled sections of the fragmented river mean that riverbank sections which are already well-covered with vegetation receive more input of new drift material and diaspores than less vegetated sections. Most of the drift material could also be produced locally, as denser vegetation increases the amount of litter produced. This relationship was not observed in the free-flowing river, but emerging objects are known to be important for trapping water-dispersed drift (Schneider and Sharitz, 1988; Skoglund, 1990).

Third, the timing of dispersal is important for the success of newly established individuals and the maintenance of species richness (Grubb, 1977). In the free-flowing river, diaspores are caught by the floodwater in spring, transported downstream and deposited when the water level drops. Areas of bare soil, including newly deposited sediment and debris, thus become available for establishment (Miller *et al.*, 1995; Auble *et al.*, 1997), and diaspores can germinate and establish during the summer season, usually in the absence of further floods. This situation optimizes the chances for seedlings to become established. In a regulated river, this situation does not occur, and diaspores can potentially reach the water at any time during the year. That is not necessarily a disadvantage, as diaspores with good floating capacity may

get more than one chance of reaching a suitable spot for establishment. However, the risk of a newly established plant to be flooded during the growing season is high.

Some populations of water-dispersed species may depend on a continuous input of diaspores in order to achieve long-term survival. The situation along a river can be viewed as an example of source–sink dynamics (Pulliam, 1988; Eriksson, 1996), where the rapids function as sources (erosion areas) and the slow-flowing stretches as sinks (deposition areas). Rapids are known to be more species-rich than slow-flowing stretches (Nilsson and Holmström, 1986), so there is a good potential for emigration. In impounded rivers, where dams are built on the rapids, which disappear, such source–sink dynamics are discontinued. Diaspores landing on an ice-covered river can potentially be transported long distances by wind, both upstream and downstream, but the dams probably also function as barriers in this case. The resulting isolation of remaining populations is likely to cause a deterioration, both in the number of individuals and in the genetic diversity (Soulé, 1986; Young *et al.*, 1996).

A possible weakness of our study is that data from only one free-flowing and one regulated river are included. However, given that the free-flowing river had ten times more drift material and twice as many drifting species, the results most likely describe an effect of regulation. To provide a fuller understanding of the effects of dams on the capacity of rivers to disperse species downstream, future studies should repeat our comparison for other rivers too, incorporating other floras and environmental settings, and also other types of regulatory schemes.

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