

Connecting variation in vegetation and stream flow: the role of geomorphic context in vegetation response to large floods along boreal rivers

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Summary

1. Flooding governs riparian plant diversity along boreal rivers but the ecological role of extreme floods is only partly understood. We studied the dynamics of riparian plant composition and richness in the free-flowing Vindel River in northern Sweden, and the importance of reach type in sustaining high species richness.

2. We conducted three surveys of riparian plant species richness over a period of two decades. The first and last of these surveys were conducted 1–3 years after significant flooding and the second was carried out after a period of more moderate flooding.

3. Our results suggest that extreme floods reduce riparian plant species richness in tranquil (slow-flowing) reaches but that a subsequent period of less extreme flood events facilitates recovery. Tranquil river reaches were also more prone to invasion by ruderal species following major floods. Species richness in turbulent reaches (rapids and runs) remained constant during all surveys. One possible explanation for this pattern is that tranquil reaches become more anoxic during floods because they have more fine-grade soils with lower hydraulic conductivity than turbulent reaches. Anoxic conditions may cause stress and plant death, opening up space for colonization. Turbulent reaches maintain a better oxygenation in the root zone of plants through high groundwater turnover, reducing negative effects of prolonged floods.

4. The fact that turbulent reaches preserved species richness regardless of flood magnitude suggests that they are important for the resistance of riparian ecosystems to prolonged inundation. In contrast, tranquil reaches, with a higher water-holding capacity, might instead maintain their species richness during drought periods.

5. *Synthesis and applications.* Our findings highlight the importance of spatial and temporal variation in riverine plant species richness and composition. To conserve these habitats at a landscape scale, a full range of reach types is necessary to allow for recovery in reaches where species richness has declined. To maintain healthy riparian zones, river managers should focus restoration efforts on interactions between hydrology, geomorphology and biota.

Key-words: anaerobic, extreme floods, oxidation reduction potential, plant diversity, redox, resistance, riparian vegetation, river, tranquil reaches, turbulent reaches

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Introduction

Riparian zones often represent local areas of high species richness (Naiman & Décamps 1997) and in most rivers this is sustained by a combination of seasonal flooding, fluvial disturbances and interannual flow variability (Junk, Bayley & Sparks 1989). During recent decades, it has become increasingly clear that certain components of the natural flow regime of a river are vital to the health and characteristics of riverine ecosystems (Poff *et al.* 1997; Richter & Postel 2004). Environmental flow management has developed from early, simplistic models of minimum flows designed to maintain individual species to more comprehensive models that consider multiple ecosystem components through linking flow and ecosystem variables (Tharme 2003). A better understanding of ecosystem responses to changes in the magnitude, timing, duration and frequency of flow and the mediating effects of channel morphology will enable us to fine-tune ecological flows and develop more sophisticated management strategies. We describe the responses of a natural riparian ecosystem to extreme floods of various durations and discuss the management implications of our results.

Extreme floods may scour and uproot riparian trees and understorey plants, saturate soils, thus altering the physical environment for organisms in the flooded zone, and change hydraulics and the distribution of material within the riparian corridor (Molles *et al.* 1998; Friedman & Auble 1999). Extreme flooding during the growing season influences vegetation more than autumn and winter flooding because it affects plant growth and development (Newbold & Mountford 1997; Johansson & Nilsson 2002). In general, species at higher elevations above the channel within the riparian zone are less adapted to submersion and water logging of soils than species in the lower parts of the riparian zone closer to the channel (Blom & Voeselek 1996; Lenssen *et al.* 1999; Merritt & Cooper 2000; Larcher 2003). However, flood-intolerant species may colonize lower altitudes during periods between significant floods. The advance and retreat of certain species may thus be predictably mediated by the relationship between the plant's autecology and the hydrological patterns (Auble, Scott & Friedman 2005).

When soils become waterlogged, oxygen is rapidly depleted through the combined effects of obstructed gas exchange, plant uptake of oxygen through plant roots, soil microbial activity and chemical processes. Depending on temperature and respiration activity, the onset of anaerobic reduction processes may take hours to days (Pezeshki 1994). The reduced ions produced in the rhizosphere in this process may be toxic to some plants. Changes in the soil physicochemical properties that accompany ion-reducing conditions are best reflected in the oxidation–reduction potential (ORP). The intensity of soil redox potential has considerable influence on plant functioning and growth, although the critical intensity is species specific (Pezeshki & DeLaune 1998).

Many plants growing in regularly flooded riparian areas do possess adaptations to anoxia (Larcher 2003), nevertheless, 'as a rule, the majority of plants succumb more quickly to flooding than to desiccation' in areas that receive ample precipitation (Larcher 2003).

One important process that affects the soil ORP is hydraulic conductivity (K), which governs the rate that a soil can conduct moving water (Davis & DeWiest 1966). Coarse substrates (with high K) potentially contain less stagnant water because of a high turnover of oxygenated water relative to that of finer-textured soils. The degree of submergence is an important determinant of plant responses to flooding; water logging of the root zone and complete submergence of above-ground portions of plants may obstruct gas exchange for non-aquatic plants. Complete inundation is shown to be more harmful to plants than mere soil inundation or partial submergence (Grimoldi *et al.* 1999; Mauchamp, Blanch & Grillas 2001). The effect of anoxia on plants is species-specific, and the individualistic responses of species affect community composition in somewhat predictable ways. Some riparian species have effective anaerobic respiration, while others can endure only very short periods of inundation, as reflected in the typical vegetation zones along rivers (Keddy 1989; Auble, Friedman & Scott 1994).

Our data set, which spanned two decades of vegetation surveys along the Vindel River in northern Sweden (Fig. 1), represented species composition and richness recorded on three different occasions, where two were recorded 1–3 years after extreme and prolonged floods, and one was recorded in a period when flooding was closer to average conditions. While more frequent, low-magnitude floods are necessary for maintaining riparian communities, we asked whether large floods that inundate the entire riparian zone and its vegetation for extended periods of time reduce species richness. We hypothesized that the plant species richness response to prolonged flooding would differ between the two major types of morphologically and hydraulically distinct reaches represented in this river: tranquil and turbulent. Tranquil reaches are often associated with a wide, low-gradient river channel with slow flow relative to narrower, steeper turbulent reaches. The riparian zones in tranquil reaches are often wide and developed on deposits of fine material (fine sand, silt and clay). Turbulent reaches usually have a narrow, sometimes multibranched channel, a steep slope and rapid flow. The riparian zone in turbulent reaches may be narrow and usually consists of coarse bed and bank material such as cobbles, boulders and coarse sand (Nilsson *et al.* 2002). Water surface slopes on tributaries of the Vindel River range from 0.01% to 0.2% along tranquil reaches and from 0.4% to 3.3% along turbulent reaches (Nilsson *et al.* 2002). These slopes corresponded well with measurements taken on several tranquil and turbulent reaches of the Vindel River, which averaged 0.0095% on tranquil reaches and 0.45% on turbulent reaches (D. Merritt, unpublished data).

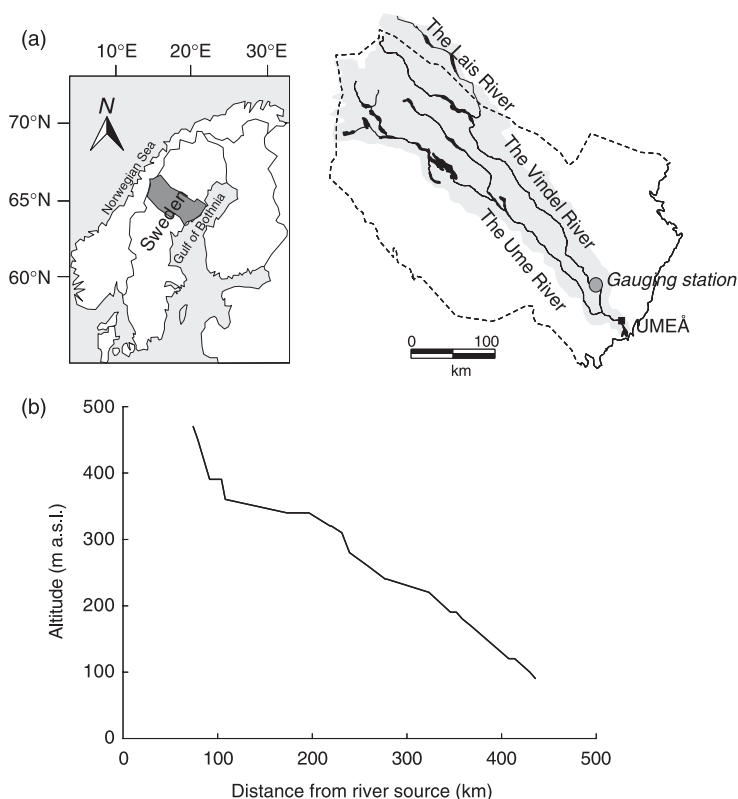


Fig. 1. (a) The Vindel River in northern Sweden and the location of the gauging station used for this study; (b) altitudinal gradient of the river, from headwaters to the confluence with the Ume River.

We anticipated that species richness would decline in tranquil reaches in years following high magnitude and/or long-duration floods and recover during intervening years, but that biota in turbulent reaches would be more resistant to long periods of inundation. Because we were working with historical species richness data, we tested the assumption that the hydrological connectivity of the substrate and thus the oxygen availability in flooded soils would differ between tranquil and turbulent reaches using a subset of river reaches representing both types. Flooding creates patches where opportunistic species and poor competitors can colonize (Keddy 1989) and severe flooding can increase the cover of non-native invasive species and annual herbs (Pettit, Froend & Davies 2001). The Vindel River is virtually free from non-native invaders but ruderal species, i.e. weeds that are good colonizers of bare substrates, may respond similarly to disturbance by flooding (Nilsson *et al.* 1989). Because we expected a differentiation in flooding effects in tranquil vs. turbulent reaches, we hypothesized that the number of ruderal species would differ between these two classes of river reaches after periods of prolonged flooding.

Methods

STUDY SITE

We worked in the seventh-order, free-flowing Vindel River in northern Sweden (Fig. 1a). The catchment of

this river comprises 12 654 km², 5% of which is lake surface. The river is 455 km long between the headwaters and the confluence with the regulated Ume River 30 km from the Gulf of Bothnia. The river drains mountain peaks with an altitude of up to 1599 m and the main river channel ranges between 80 and 1000 m a.s.l. The river has a stepwise profile with alternating turbulent and tranquil reaches, and the gradient of the river is fairly continuous between the mountains and the coast (Fig. 1b). The measured discharge in the lower reaches varies between 15 m³ s⁻¹ in late winter and > 1700 m³ s⁻¹ in early summer, with an annual mean of 180 m³ s⁻¹. The river channel is ice-covered during winter, and ice forms at levels below the riparian zone. During spring, ice breaks up and disappears in this river, usually without jamming and damaging riparian vegetation. The range of flood height, relative to the summer low-water level, is between 1.2 and 4.6 m in the studied portions of the main channel (Sundborg, Elfström & Rudberg 1980). The width of riparian zone ranges from 6.6 to 150.0 m in the main channel.

Bank substrate is predominately of morainic origin along the upper reaches of the main channel, and silt and sand along the lower reaches. The transition between these two substrate types represents the highest level of the former Ancylus Lake, a freshwater prestage of the present Baltic Sea that was formed after the most recent deglaciation. Because of crustal rebound the distance between this former highest coastline and the present coast is continuously increasing. The river-bank vegetation along the Vindel River is distinctly vertically zoned at any given location, with transitions from forest communities furthest from the channel, to shrub vegetation, to herbaceous communities nearer the channel. At a species level, an average riverbank along the main channel may show the following sequence of dominants (from high to low altitude): *Pinus sylvestris*, *Vaccinium vitis-idaea*, *Alnus incana*, *Calluna vulgaris*, *Molinia caerulea*, *Salix lapponum*, *Carex juncella* and *Ranunculus reptans* (species nomenclature follows Krok & Almqvist 1994 throughout the paper).

SAMPLING

We surveyed the riparian vegetation and environment of tranquil and turbulent sites along the Vindel River in 1978, 1988 and 1997–98 [1978, $n=26$, 19 tranquil/seven turbulent; 1988, $n=23$, 16/7; 1997–98, $n=53$, 28 (in 1997)/25 (in 1998)]. There was no significant difference either in mean distance from river source or in mean altitude of the tranquil and turbulent sites in any of the study years (Table 1). These years represented conditions shortly after and between two major floods. We defined major floods as those exceeding 1000 m³ s⁻¹ and exceeding 10 days of inundation. Each site consisted of a 200-m long reach spanning the entire width between the spring flood high, i.e. the highest level attained at least once every 2 years, and summer low levels. In most

Table 1. Comparisons of mean altitude and mean distance from headwaters between the tranquil and turbulent reaches of the Vindel River in northern Sweden used in the vegetation surveys in 1978, 1988 and 1997–98

Variable	Tranquil		Turbulent		<i>P</i> *
	Mean	SE	Mean	SE	
1978					
Distance from river mouth (km)	311	17	299	38	0.74
Altitude (m a.s.l.)	223	15	229	38	0.87
1988				48	0.66
Distance from river mouth (km)	247	32	221	61	0.44
Altitude (m a.s.l.)	285	34	336		
1997/1998				24	0.65
Distance from river mouth (km)	282	13	269	23	0.47
Altitude (m a.s.l.)	238	11	257		

*Independent samples *t*-test.

cases, the spring high-water level was judged equivalent to the lower end of continuous occurrences of flood-intolerant species such as *Vaccinium myrtillus*. Upland vegetation is generally species poor compared with riparian zones, making the exact delimitation of the riparian zone less critical. As the width of the riparian zone differed between sites, we assessed species–area relationships to evaluate whether species richness data should be corrected for area. Such transformations have been found useful in similar studies (Nilsson *et al.* 1989) but in this case we found no relationship between species richness and area at the scale sampled. Therefore we used absolute data for species richness throughout the study.

VEGETATION

Two people independently recorded all vascular plant species growing within each reach, and species lists were combined. Each sampling year, new sets of sites were distributed along the river, from headwater to coast, and classified using visual evaluation of current velocity in the field. Rapids and runs were classified as turbulent and slow-flowing reaches as tranquil. We also estimated the percentage cover of trees plus shrubs (individuals of woody species > 0.25 cm) and dwarf shrubs (< 0.25 cm) plus herbs. This was made by visual estimation independently by two people; final cover values were reached by consensus. Frequencies of species were calculated as the number of reaches in which a species occurred divided by the total number of reaches.

ENVIRONMENT

At each site we determined the mean width (average of five widths measured at 50-m intervals; not measured in 1978) and height (in the middle of the reach, measured with a stadia rod and level) of the riparian zone. The riparian zone was defined as the entire width between the spring flood high stage (the highest level

attained at least once every 2 years) and summer low levels. We also measured the number and percentage cover of substrate types along the reach. The percentage cover of substrate was estimated by visual estimation independently by two people; final cover values were reached by consensus. Nine substrate types were identified, reflecting the Wentworth size classes clay, silt, sand, gravel, pebbles, cobbles and boulders (Chorley, Schumm & Sugden 1984), supplemented by peat and bedrock. Substrate fineness (Φ -value) was calculated as the sum of the log₂-transformed grain size for each substrate size class weighted according to the proportion of the river margin occupied by that class (Wright *et al.* 1984; Nilsson *et al.* 1989). Substrate type cover was estimated by two people independently and final percentages were reached by consensus.

We measured the ORP of riparian soils in both tranquil and turbulent reaches. Paired tranquil and turbulent reaches occurred along the entire studied reach of the Vindel River and possessed similar characteristics. Because lateral zonation of the vegetation (see above) was distinct and consistent along the studied reaches of the Vindel River, the redox measurement sites were representative of the vegetation. At the ORP sites, we installed probes at the transition between the herbaceous and shrub zone, which represented intermediate conditions across the riparian zone. In mid-June 2001, 96 calibrated platinum-tipped electrodes were installed at six sites along the river. Peak flow in 2001 (898 m³ s⁻¹) reflected the long-term peak flow average for the Vindel (905 m³ s⁻¹) and occurred between 16 and 17 June. Four sets of paired probes were placed randomly along 200-m long transects along the herb–shrub zone transition. Probe tips were inserted to a depth of 15 cm and left in place for the remainder of the measurement period (to September 2001). ORP (to the nearest mV) was measured six times in each of these sites immediately following the recession of peak flows, using an Orion model 290 A portable pH meter (Orion Research Inc., Beverly, MA). We calculated reach-average hydraulic conductivity for tranquil and turbulent reaches from the 1997–98 data

particle-size distribution data using the Kozeny–Carmen Bear equation (Freeze & Cheery 1979; Domenico & Schwartz 1998). Particle size distributions were developed from substrate data gathered during field surveys.

FLOODING HISTORY

The magnitude of recurrent seasonal floods differed between years but most floods tended to fall within the same range (mean ± 1 SE; maximum discharge 1911–1998, 916 ± 253 m³ s⁻¹; location of the gauging station shown in Fig. 1a). The river experienced several major floods in the 20th century (Fig. 2). All major floods occurred after the onset of the growing season, when most plants had broken winter dormancy. The latest of these floods (1995) reached the highest discharge ever measured in the river, with a flow exceeding 1700 m³ s⁻¹, i.e. nearly twice the average annual maximum flow. Floods with a discharge > 1000 m³ s⁻¹ inundate most of the riparian zone along the reaches (B. Renöfält, personal observation). Such floods occur at a recurrence interval of approximately 3 years (Fig. 2) but rarely last longer than a few days (mean duration ± 1 SE; of floods > 1000 m³ s⁻¹ in the period 1971–1998, 2 ± 0.6 days). In 1977, the year preceding the 1978 vegetation survey, discharges > 1000 m³ s⁻¹ lasted 8 days, and in 1995, the major flood preceding the 1997–98 vegetation survey, discharges > 1000 m³ s⁻¹ lasted 13 days. During the 8-year period before the 1988 survey, discharges > 1000 m³ s⁻¹ occurred three times but only lasted for 3–4 days each time. Floods > 1170 m³ s⁻¹ completely submerge all ground vegetation less than 0.5 m in height in this particular system. Floods of this magnitude occurred 10 times during the 20th century (Fig. 2). Floods in 1977 and 1995 far exceeded the duration of the floods during the 1980s, and the magnitude of the 1995 flood exceeded any given record for the Vindel River. The frequency of large floods during the period 1971–98 was either 0 or 1, i.e. there was never more than one large flood per year. All floods occurred between mid-May and late June.

DATA ANALYSIS

We used Hochberg's GT2 method (Sokal & Rohlf 1995) for multiple comparisons with unequal sample sizes following ANOVA to test whether species richness differed between years. Within-year differences in species richness and differences in environmental variables between tranquil and turbulent reaches were tested using a two-tailed *t*-test. We adjusted for multiple *t*-tests using a Bonferroni adjustment (maintaining a significance of $P = 0.05$; Holm 1979).

Differences in the frequency of 315 riparian species between tranquil and turbulent reaches for 1978, 1988 and 1997–98 were evaluated using principal components analysis (PCA). Axes of the PCA represent frequency rather than abundance of species. PCA was conducted using a correlation matrix on the differences

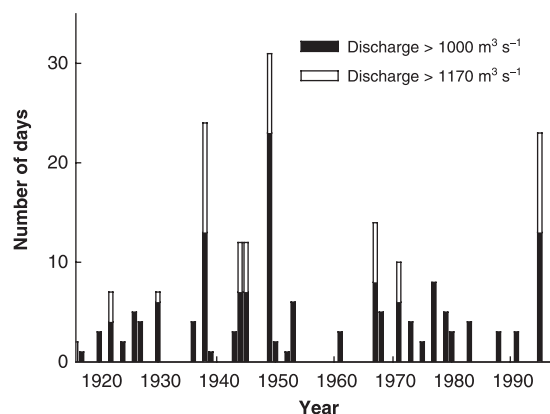


Fig. 2. Duration of high discharges in the Vindel River during the period 1911–98. Black bars show duration of discharges > 1000 m³ s⁻¹ that inundate the entire riparian ground, and white bars those > 1170 m³ s⁻¹ that inundate all riparian vegetation of < 0.5 m height. The mean annual discharge of the river was 180 m³ s⁻¹. Discharge data from the Granåker gauging station (location shown in Fig. 1a).

in frequency. Weightings of species on each of the axes were evaluated and those with the highest weightings reported.

We evaluated similarities in plant communities between years and between reach types using analysis of similarity (ANOSIM). ANOSIM is broadly analogous to analysis of variance. Tests of within- and between-group similarity were conducted, in this case inter- vs. intragroup similarities were formally tested and compared with randomly assigned groups (999 permutations). Tests for differences between groups were conducted through calculating an *R* statistic (ranging from -1 to 1) and through calculating a *P*-value from permutations of randomly assigned groups. An *R* of 1 indicates complete differences in species composition between groups (years and reach types) and an *R* of 0 indicates no difference between groups (negative *R* would indicate that similarities between groups are greater than within a group). *P*-values were from a permutation test of the null hypothesis of no difference between groups. Bray–Curtis similarity matrices were used for ANOSIM.

We used a Fisher's exact test to explore whether ruderal species in turbulent and tranquil reaches deviated from the expected value based on the total proportion of ruderals. This was undertaken for all sampling years. Differences in ORP were tested with Tukey's test following ANOVA and differences in hydraulic conductivity between tranquil and turbulent reaches were tested with a two-tailed *t*-test. To assess the risk of committing type II errors, we calculated the power of the statistical tests. When statistical power was low, the least detectable difference between samples was calculated. For the statistical tests we used SPSS version 11.0 (SPSS Inc., Chicago, IL) and SAS release 8.1 (SAS Institute Inc., Cary, NC). The PCA was performed in SAS version 8.1 using the correlation matrix. Statistical power and least detectable difference were

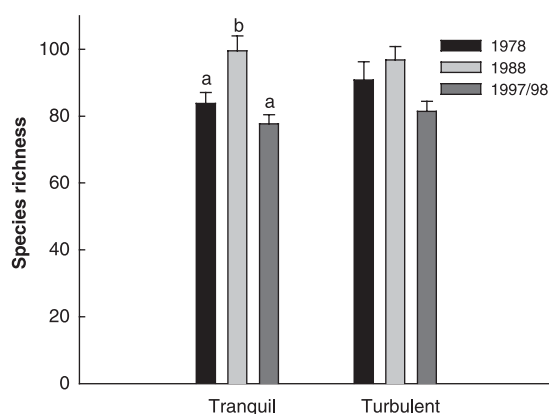


Fig. 3. Mean species richness along the Vindel River differed significantly between years in tranquil but not in turbulent reaches. Letters indicate statistically significant differences (Hochberg's GT2 method for multiple comparisons with unequal sample sizes following ANOVA). (a,b) $P < 0.001$.

calculated using PASS version 6.0 (NCSS Statistical Software, Kaysville, UT). ANOSIM was conducted using Primer version 5.2.9 for Windows (PRIMER-E Ltd, Plymouth, UK; Clark & Gorley 2001).

Results

VEGETATION

We found less variation in species richness between years in turbulent than in tranquil reaches (Fig. 3). Species richness in tranquil reaches was significantly lower in 1978 ($P = 0.011$) and 1997–98 ($P < 0.001$) than in 1988, and there was no significant difference ($P = 0.44$) between 1978 and 1997–98. Although the statistical power was low (0.18) between 1978 and 1988 because of a small sample size, the least detectable difference (15.90 species) did not differ significantly from the difference found in tranquil reaches (15.72 species). In turbulent reaches, there was no statistically significant difference between years (1978 and 1988, $P = 0.81$; 1988 and 1997–98, $P = 0.051$; 1978 and 1997–98, $P = 0.33$; Fig. 3). This indicated that species richness responded to flooding in tranquil but not in turbulent reaches.

An analysis of the frequency distribution for the entire river revealed that almost twice as many species increased as decreased during the 'recovery period' of 1978–88 (Table 2). During the 'depletion period' between 1988 and 1997–98 (effects of flooding in 1995), three

times more species decreased than increased. In tranquil reaches the net gain of species during the recovery period was 61, compared with 33 in turbulent reaches. During the depletion period, the net loss of species was 93 in tranquil compared with 44 in turbulent reaches. Floods affected the frequency distribution of all species in both types of reaches.

Seventy per cent of the variability in vascular plant frequency was explained by the first three axes in the PCA. The ordination revealed that the community composition in tranquil reaches was more severely affected by flooding than in turbulent reaches but that species composition returned to pre-flood conditions within a decade of a major disturbance (Fig. 4). Turbulent reaches, on the other hand, were less affected but were generally more variable in species composition through time. *Bartsia alpina*, *Carex aquatilis*, *Parnassia palustris*, *Pyrola minor*, *Selaginella selaginoides*, *Vaccinium myrtillus*, *Viola biflora* and *Saussurea alpina* were all strongly positively weighted on PCA axis 1. *Calamagrostis canescens*, *Convallaria majalis*, *Capsella bursa-pastoris*, *Ribes nigrum*, *Stellaria graminea*, *Silene vulgaris*, *Erysimum cheiranthoides*, *Alopecurus aequalis*, *Carex acuta* and *Lathyrus pratensis* were species that were heavily negatively weighted on axis 1. PCA axis 2 was driven largely by *Calamagrostis epigeios*, *Melica nutans*, *Eleocharis mamillata*, *Calamagrostis lapponica*, *Trifolium repens*, *Salix hastata*, *Lychnis alpina*, *Trifolium pratense* and *Epilobium angustifolium*, which were all positively weighted. Species with low scores on axis 2 included *Carex limosa*, *Carex livida*, *Carex rhyncho-physa*, *Carex saxatilis*, *Epilobium hornemannii*, *Euphrasia stricta*, *Gnaphalium supinum* and *Saxifraga stellaris*. In turbulent reaches, ruderal species numbers remained relatively low and stable and, in relation to total numbers of ruderals for the entire river, they were significantly underrepresented in 1978 and 1997–98 (Table 3). In tranquil reaches, the mean number of ruderal species fluctuated between years, with higher counts following flood years (1978 and 1997–98). In 1988, the mean number of ruderal species in tranquil reaches was low, equalling the counts for turbulent reaches (Fig. 5).

ANOSIM revealed that community composition differed significantly between tranquil and turbulent reaches averaged over years ($R = 0.30$, $P = 0.001$) and between years averaged over reach type ($R = 0.16$, $P = 0.002$). When ANOSIM was conducted to test for differences in species composition between tranquil and turbulent

Table 2. Changes in the frequency of riparian plant species in the Vindel River in northern Sweden during the period 1978–88, when vegetation recovered after the major 1977 flood, and the period 1988–1997–98, during which vegetation was affected by the 1995 flood. Data are number of species and mean change (%) per species

Period	Turbulent reaches			Tranquil reaches			All reaches		
	Gains	Losses	Unchanged	Gains	Losses	Unchanged	Gains	Losses	Unchanged
1978–88	100 (23)	67 (24)	90	166 (16)	105 (9)	17	87 (23)	45 (11)	4
1988–1997–98	99 (11)	143 (18)	14	85 (9)	178 (17)	25	31 (7)	103 (19)	2

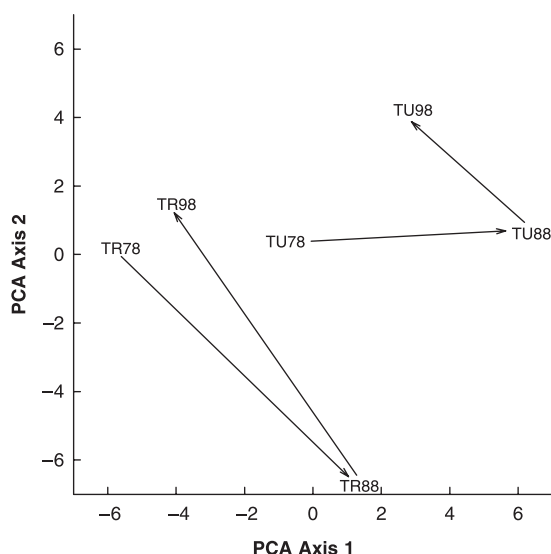


Fig. 4. Principal components analysis of tranquil (TR) and turbulent (TU) reaches in 1978, 1988 and 1997–98 in the Vindel River. Variables used in the analysis were frequency of each of 315 vascular plant species in all sampled reaches on each year of observation. PCA axes 1 and 2 accounted for 31% and 21%, respectively, of the variation in the species data. Arrows represent the direction of change in the reach type through time.

reaches for each year individually, species composition significantly differed in 1998 ($R = 0.43$, $P = 0.001$) but not in 1978 ($R = 0.11$, $P = 0.156$) or 1988 ($R = 0.035$, $P = 0.344$). This indicated that tranquil and turbulent reaches were most similar in 1988 (after mild flooding in 1987) and least similar in 1998, and to some extent in 1978, after higher magnitude and longer duration flooding. Ninety per cent of the difference between reach types in 1998 was accounted for by only 76 (24%) of the 315 species. The 10 species that most influenced differences between tranquil (TR) and turbulent (TU) reaches were *Salix borealis* (TR), *Ranunculus reptans* (TR), *Veronica scutellata* (TR), *Parnassia palustris* (TU), *Prunella vulgaris* (TU), *Cirsium helenioides* (TU), *Carex vesicaria* (TR), *Antennaria dioica* (TU), *Melampyrum sylvaticum* (TR) and *Pedicularis palustris* (TR). Tests were also conducted to compare species composition

Table 3. Actual numbers in relation to expected numbers of ruderals in riparian zones along turbulent and tranquil reaches of the Vindel River. Expected numbers are calculated based on the total number of ruderal species irrespective of reach type, for each year. Fisher's exact test, two-tailed probability. Significant differences are in bold

	d.f.	Expected count	Actual count	Deviance	P
1978					
Turbulent	1	16.6	5	-11.6	0.0001
Tranquil	1	21	20	-1	0.25
1988					
Turbulent	1	6.1	4	-2.1	0.094
Tranquil	1	7.6	8	+0.4	1
1997–98					
Turbulent	1	14.2	8	-6.2	0.0004
Tranquil	1	13.3	15	+1.7	0.24

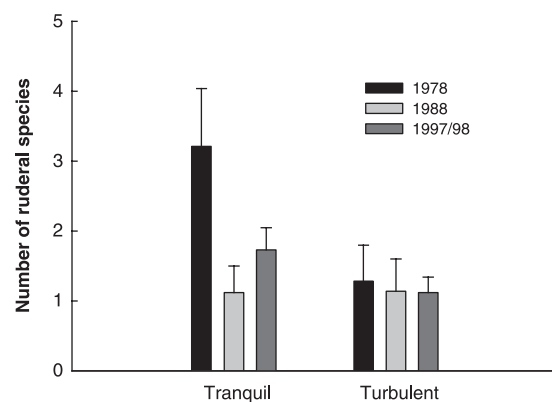


Fig. 5. Mean numbers of ruderal species in tranquil and turbulent reaches. In tranquil reaches, the mean number of ruderal species fluctuated between years, with higher counts following flood years (1978 and 1997–98). In 1988, the mean number of ruderal species in tranquil reaches was low, equalling the counts for turbulent reaches.

between years in turbulent reaches ($R = 0.042$, $P = 0.330$) and between years in tranquil reaches ($R = 0.232$, $P = 0.001$). There were significant differences in species composition in tranquil reaches between all pairwise sets of years ($P = 0.001$), indicating highly dynamic communities through time in tranquil relative to turbulent reaches.

ENVIRONMENT

We compared substrate heterogeneity, substrate fineness, river margin area and river margin height between tranquil and turbulent reaches using the 1997–98 data (Table 4). Turbulent reaches were more heterogeneous than tranquil ones, and tranquil reaches had a wider river margin and finer textured substrate (i.e. a higher water-holding capacity). None of these environmental factors correlated with species richness in reach type. Riparian soils were anoxic (ORP < 400 mV) on all measurement dates in both reach types (Fig. 6). The riparian soils measured were inundated continually from 8 June to 15 July 2001. The lowest level of ORP occurred after the fourth continuous week of inundation. Mean ORP levels reached a minimum of -62 mV in tranquil reaches (the extreme low was -433 mV in a tranquil reach). Sulphur-reducing bacteria are favoured between -50 and -200 mV and methanogenesis occurs at approximately -200 mV (Mitch & Gosselink 2000). In turbulent reaches, soil oxidation reached its minimum ORP at the same time as tranquil reaches but this level was more than 80 mV higher than in the tranquil reaches and well above the level at which sulphur (toxic to plants) reduces. Soil ORP was lower by an average of 66.8 mV in tranquil relative to turbulent reaches on all measurement dates (Fig. 6). Anoxia was significantly more severe in tranquil than in turbulent reaches on three of the five measurement dates. The rates of the onset of recovery from anoxia also differed between the two types of reaches, although these differences were

Table 4. Comparisons of environmental factors between tranquil and turbulent reaches in the 1997–98 riparian sites in the Vindel River. Significant differences are in bold

Variable	Tranquil (<i>n</i> = 28)		Turbulent (<i>n</i> = 25)		<i>P</i> *
	Mean	SE	Mean	SE	
Environmental factors					
Number of substrate types	2.50	0.32	4.04	0.30	0.001
Overall substrate calibre (Φ)†	5.06	0.36	–2.00	0.77	< 0.0001
Area of river margin (m ²)	8503.7	1570.0	3829.0	582.4	0.009
Height of river margin (cm)	217.8	15.72	209.1	9.5	0.64
River margin slope vegetation cover					
Herbs + dwarf shrubs (%)	49.8	3.8	62.7	4.8	0.038‡
Trees + shrubs (%)	56.3	4.1	47.2	3.8	0.11

*Independent samples *t*-test.† Φ -value calculations after Wright *et al.* (1984).

‡Not significant after Bonferroni correction using a sequential procedure (Holm 1979).

not statistically significant. The rate of onset of anoxia during 2–4 July was -61.7 and -63.4 mV day⁻¹, and the rate of recovery from anoxia during 9–27 July was 10.6 and 10.4 mV day⁻¹ in tranquil and turbulent reaches, respectively. Because the soil in turbulent reaches is typically coarser and better drained, we expected a higher rate of recovery from anoxia there than in the finer textured and less permeable soils in the tranquil reaches. Hydraulic conductivity of turbulent reaches was significantly higher ($P < 0.003$) than in tranquil reaches (Fig. 7).

Discussion

Seasonal flooding is commonly recognized as a key determinant of species richness in riparian systems. It structures species richness and composition in the riparian corridor, and regulated rivers that are deprived

of their natural flooding regime have fewer species than comparable free-flowing rivers (Jansson *et al.* 2000). Large floods shape the physical habitat and rejuvenate the system, controlling the distribution and abundance of floodplain plants in areas that are seasonally inundated. We asked how riparian vegetation would respond to floods that could be considered extreme for a river system, and whether vegetation along reaches with inherent physical differences would react in distinct ways to extreme flooding. Our results show that mean species richness was temporally variable in tranquil reaches of the free-flowing boreal Vindel River but remained stable in the turbulent reaches (Fig. 3), and that species turnover was higher in tranquil compared to turbulent reaches. This suggests that long-lasting floods reduce local plant species richness at the tranquil riparian sites but that vegetation recovers between major floods. We do not know the recovery time of these communities, but species richness increased significantly within a 10-year period following flooding, suggesting that plant recolonization may be relatively fast.

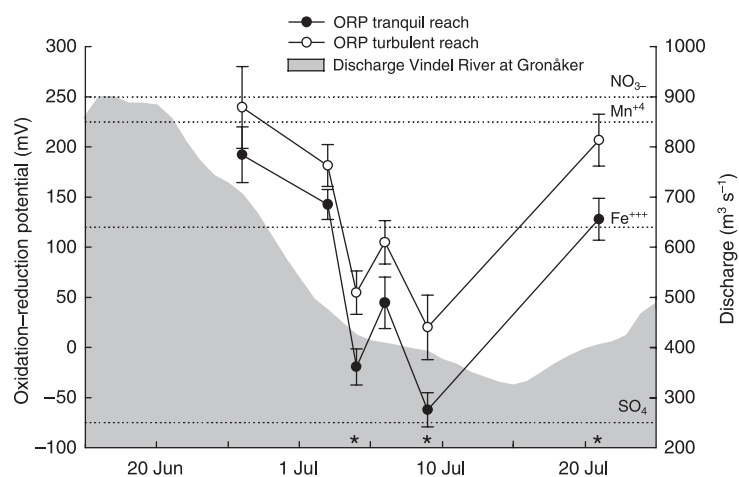


Fig. 6. Mean levels of oxidation–reduction potential (ORP) in riparian sites along the Vindel River measured at five times following the snowmelt peak of the hydrograph in July 2001. Asterisks (*) at the bottom of the plot indicate statistically significant differences between mean ORP in tranquil and turbulent reaches ($P < 0.05$, Tukey's test following ANOVA). Horizontal dotted lines indicate the ORP levels at which various elements become reduced. Bar plot shows the difference in ORP in tranquil and turbulent reaches at each measurement date. Area plot shows the river discharge (m³ s⁻¹) during the measurement period (Grönåker gauging station).

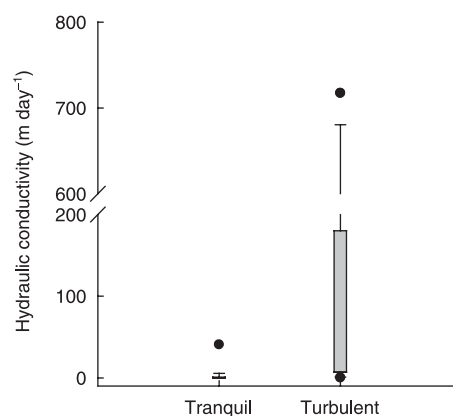


Fig. 7. Mean difference in hydraulic conductivity (m day⁻¹) between riparian sites of tranquil and turbulent reaches of the Vindel River. The lower boundary of the box represents the 25th percentile and the upper boundary the 75th percentile. Whiskers below and above the box indicate the 10th and 90th percentiles, respectively; dots are outliers.

The reason for differences in temporal variability between tranquil and turbulent reaches (Figs 3 and 4) remains unclear. It could be that suites of flood-intolerant species drove the high values of species richness in tranquil reaches in 1988. However, an analysis of species that only occurred in single years did not identify 1988 as a year with more specific or functionally different species than other years. This may be because propagule dispersal can vary considerably between years (Andersson & Nilsson 2002), leaving it partly to chance which species will be found in a specific reach in any given year. Observations suggest that flood-intolerant species may sometimes grow at lower positions in the riparian zone in turbulent than in tranquil reaches (Nilsson 1979). A study in the Vindel River (M. E. Johansson, personal communication) revealed that *Carex canescens* occurred in sites inundated < 75 days year⁻¹ in tranquil and 60–120 days year⁻¹ in turbulent reaches. Another example is *Juncus alpinus*, which grew in sites inundated 60–80 days year⁻¹ in tranquil and 60–120 days year⁻¹ in turbulent reaches. This is probably because of inherent differences in the physical characteristics of the two reach types.

Turbulent reaches were more resistant to anoxia during flooding (Fig. 6), probably because of a higher hydraulic conductivity (Fig. 7). These results indicate that reduced oxygen depletion in specific habitats might be important for plants during prolonged floods and associated waterlogging of the soil. There are two possible explanations for this: (i) the coarser the substrate, the more hydraulically conductive the substrate is, resulting in higher turnover of groundwater and oxygenated surface water and increased connectivity between surface and shallow groundwater; and (ii) finer sediment and silt may contain more organic material than sand and gravel, and therefore consume more oxygen during decomposition than coarser material. The mechanisms behind more stable species richness in turbulent reaches might therefore correlate with flooding effects, and specifically oxygenation of the riparian substrate. Dwire *et al.* (2004) found that the ORP was negatively correlated with vegetation biomass along streams in north-east Oregon, USA. Although these sedge-dominated meadows are relatively species poor, richness increased at higher elevations in more aerated soils (higher ORP). Scott, Lines & Auble (2000) suggested that site history of hydrological fluctuation affects plant growth and root development. A riparian site affected by dramatic seasonal fluctuations in the river stage facilitates the development of extensive root systems in *Populus*. The same species growing in the same climate but on a riparian site along a stream with more stable water tables produced shallow, poorly developed root systems. *Populus* growing along a fluctuating stream would be less susceptible to drought than *Populus* growing along a relatively stable stream. Because turbulent sections are narrower, water table fluctuations should be more extreme along turbulent reaches and less so along tranquil ones. It is possible

that such fluctuations cause differential root growth of the same species along turbulent vs. tranquil reaches so that the acquisition of oxygenated water is more efficient. It is also possible that differentiation in developing adaptations to flooding or anoxia, such as aerenchyma cells in the roots, could contribute to higher resistance to anoxia.

There are other mechanisms connected to flooding that can potentially reduce species richness. Decreased light availability because of suspended sediment load affects plant distribution (Vervuren, Blom & de Kroon 2003). However, this is unlikely to have a strong effect in the Vindel River, where water contains very little suspended sediment even during floods. We did not measure whether sediment deposition differed between tranquil and turbulent reaches, but the sediment mass deposited by floods in the riparian zone of this river is generally small. Mechanical stress is also important for plant mortality. During the 1995 flood, the volume of large wood transported by the river was unusually high because wood was extracted from sites not previously reached by floods (B.M. Renöfält, personal observation). It is unlikely, however, that this explains the observed patterns because turbulent reaches are subjected to a larger mechanical stress than tranquil ones and removed patches of vegetation were not evident along either type of reach. It could be, however, that vegetation in turbulent reaches is more adapted to mechanical stress through mechanisms parallel to that of extended root growth in the *Populus* example mentioned above (Scott, Lines & Auble 2000). One factor that could contribute to higher flood resistance in turbulent reaches is the fact that these reaches often have a more complex geomorphology and coarser substrate compared with tranquil reaches (Table 4). This could provide more safe sites for anchoring plants (e.g. cracks in rocks) and also play a role in oxygen availability (see above).

Differences in plant dispersal could result in higher species richness in turbulent than tranquil reaches if turbulent reaches are subjected to more river-borne material than tranquil sites. Merritt & Wohl (2002) showed that channel morphology and hydraulics affect seed deposition; eddies and slack water areas were most effective at trapping seeds under natural flow conditions. Andersson, Nilsson & Johansson (2000) found a positive correlation between propagule trapping efficiency and species richness, indicating that the ability of the riparian zone to trap seeds is important for its species richness. Nilsson *et al.* (2002) compared riparian vegetation in tranquil and turbulent reaches in seven tributaries to the Vindel River and found that the species of those reaches differed in their dispersal traits, although they did not differ in total species richness. Turbulent reaches had a significantly lower proportion of long-floating species and a significantly larger proportion of short-floating species than tranquil reaches. Even if the higher species richness in turbulent reaches in 1978 and 1997–98 was a result of a more effective propagule trapping, it is unlikely that this would be

temporally variable. In 1988, there was no statistical difference in species richness between turbulent and tranquil reaches. Mean species richness in 1988 was in fact slightly higher in the tranquil reaches. Pollock, Naiman & Hanley (1998) showed that plant species richness was positively correlated with spatial variation in flood frequency in riparian wetlands in south-east Alaska. Spatial variation in microsite flood frequency could potentially explain the higher species richness in turbulent reaches, as these are more topographically variable than tranquil ones. But again, this pattern would be likely to be stable among years if no other factor influences plant mortality. Thus our data suggest that tranquil reaches are more sensitive to plant mortality as a result of more severe anoxia along the stream reaches.

Large floods create gaps in the vegetation, thereby allowing vegetation to rejuvenate but also paving the way for colonization of opportunistic species, including non-native ones (Menges & Waller 1983). Such gaps could stem from soil erosion and removal of plant biomass by floods. The number of ruderal species in turbulent reaches remained relatively low and stable between years, whereas tranquil reaches were more variable, with more ruderal species after floods (Table 3 and Fig. 5). In years following extreme flooding, ruderal species were significantly underrepresented in turbulent reaches. In a period of less extreme floods, the overall number of ruderal species was low. This implies that extreme flooding favours colonization for opportunistic species in tranquil reaches. It also implies that turbulent reaches have inherent characteristics that may enable vegetation to withstand invasion by ruderal species.

IMPLICATIONS FOR RIVER MANAGEMENT

Riparian plant diversity decreased as a result of long floods and this decrease was more pronounced in tranquil reaches where soils became anoxic more quickly and severely. Turbulent reaches had better aerated soils and therefore their vegetation was more resistant to flooding. During periods with less flooding, riparian species richness in tranquil reaches recovered. Ruderal species responded to the prolonged floods, peaking in numbers in tranquil but not in turbulent reaches. Our findings highlight the importance of spatial and temporal variation for the dynamics of riverine plant species richness and composition. Our results further suggest that turbulent reaches are generally important for maintaining species richness during extreme floods. In contrast, tranquil reaches, with a higher water-holding capacity, might sustain their species richness during drought periods. In order to implement conservation at a landscape scale, it is necessary to keep the full range of reach types to allow for recovery in reaches that have lost species. River managers should focus restoration efforts more widely than specific species or specific processes. To maintain healthy riparian zones it is important to consider interactions between hydrology, geomorphology and biota. Unfortunately, river exploitation world-wide

has dramatically reduced the number of turbulent river reaches through dam construction (Nilsson *et al.* 2005b) and channelization (Shankman & Smith 2004; Nilsson *et al.* 2005a; Yoshimura *et al.* 2005). Recent restoration efforts, such as dam removal and channel widening through removal of dykes and piers, can thus prove to be useful tools, not only to recreate turbulent river reaches but also to increase the resilience of entire river systems.

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