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Citation for the original published paper (version of record):

Jansson, R., Nilsson, C., Dynesius, M., Andersson, E. (2000)

Effects of river regulation on river-margin vegetation: a comparison of eight boreal rivers.

*Ecological Applications*, 10(1): 203-224

<http://dx.doi.org/10.2307/2640996>

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## EFFECTS OF RIVER REGULATION ON RIVER-MARGIN VEGETATION: A COMPARISON OF EIGHT BOREAL RIVERS

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**Abstract.** Regulation and fragmentation by dams belong to the most widespread deliberate impacts of humans on the world's rivers, especially in the Northern Hemisphere. We evaluated the effects of hydroelectric development by comparing the flora of vascular plants in 200-m-long reaches of river margin distributed along eight entire rivers in northern Sweden. Four of these rivers were free-flowing, and four were strongly regulated for hydroelectric purposes. First, we compared species diversity per site between entire free-flowing and regulated rivers. To reduce the effects of natural, between-river variation, we compared adjacent rivers. One regulated river had lower plant species richness and cover than two adjacent free-flowing ones, whereas two other parallel rivers, one regulated and another free-flowing, did not differ significantly. Second, river-margin vegetation responded differently to different types of regulated water-level regimes. Both along run-of-river impoundments, with small but daily water-level fluctuations, and along storage reservoirs, with large fluctuations between low water levels in spring and high levels in late summer and fall, the number of species and their cover per site were lower than along the free-flowing rivers. Regulated but unimpounded reaches were most similar to free-flowing rivers, having lower plant cover per site, but similar numbers of species. For reaches with reduced discharge, evidence was mixed; some variables were lower compared to free-flowing rivers whereas others were not. However, for the last two types of regulation, statistical power was low due to small sample sizes. Third, we classified all plant species according to their dispersal mechanisms and tested whether they respond differently to different types of regulated water-level regimes. Three out of four types of regulation had higher proportions of wind-dispersed species, and two out of four had lower proportions of species without specific mechanisms for dispersal, compared to free-flowing rivers, suggesting that dispersal ability is critical for persistence following regulation. Run-of-river impoundments had higher proportions of long-floating species and species with mechanisms for vegetative dispersal, suggesting that water dispersal may still be important despite fragmentation by dams. Fourth, plant species richness and cover varied with both local factors, such as water-level regime, and regional factors, such as length of the growing season. Presence of clay and silt in the river-margin soil, preregulation position of the contemporary river margin, non-reservoir sites, low altitudes, and long growing seasons were associated with high plant species richness and cover.

**Key words:** dams; dispersal capacity of river-margin plants; disturbance; fragmentation; plant species richness vs. water-level regime; reservoirs; riparian vegetation; river regulation, effects on vegetation; seed dispersal; Sweden, northern; vegetative dispersal.

### INTRODUCTION

About two thirds of the freshwater flowing to the oceans is estimated to be controlled by dams (Petts 1984, Naiman et al. 1993), and in the United States, Canada, Europe, and the former Soviet Union, 85 of the 139 largest river systems, or 77% of the flow, are moderately or strongly affected by regulation (Dynesius and Nilsson 1994). River-margin communities, given their dependence on river hydrology (e.g., Day et al. 1988, Hughes 1990, Gregory et al. 1991, Naiman and Décamps 1997), inevitably change when river flow changes. However, the specific responses are difficult

to predict, because rivers are complex, dynamic ecosystems and river regulation changes hydrological and geomorphological as well as biological variables. Therefore, to understand the combined and ultimate effects of river regulation, a combination of long-term studies of postregulation conditions (e.g., Nilsson et al. 1997) and large-scale, quantitative comparisons of affected and unaffected river systems (e.g., Johnson 1994, Wootton et al. 1996) is needed. However, such studies are rare, and more knowledge is required to provide a basis for better management and rehabilitation of river systems affected by hydroelectric schemes (Nilsson and Brittain 1996).

In a previous study (Nilsson et al. 1991a), we analyzed the effects of river regulation on river-margin

vegetation by comparing one free-flowing and one strongly regulated river. Plant cover and species richness were lower in the regulated river. Furthermore, most functional groups of species were more species poor and none more species rich in the regulated river. Species richness was higher in sites with remnants of preregulation vegetation, and decreased with increasing height of the river margin. Nilsson et al. (1991a) attributed overall differences between rivers to the hydrological disruption caused by dams. A major disadvantage of such a study is that it does not allow general conclusions about the effects in other rivers. Although preregulation documentation suggested that river-margin vegetation was similar between rivers, we cannot be certain to what degree differences were due to river regulation or represented natural variation between rivers. One way of testing the generality of the previous results would be to repeat the study by comparing adjacent free-flowing and regulated rivers in other areas (Keddy 1989, Hargrove and Pickering 1992, Primack and Miao 1992b). Therefore, we compared river-margin vegetation along five other rivers, three free flowing and two regulated, to test if similar differences in river-margin vegetation would emerge.

Although the combined effects of river regulation may be difficult to predict, the time since regulation (Petts 1984, Church 1995), the disturbances from water-level fluctuations (Keddy and Reznicek 1986, Nilsson and Keddy 1988), and the conditions for colonization and establishment on the regulated river margins (Fenner et al. 1985, Hughes 1990, Rood and Mahoney 1990, Krahulec and Lepš 1994) are likely to be important factors. In a previous study we investigated the long-term development of river-margin vegetation along regulated waterbodies (Nilsson et al. 1997). Furthermore, river-margin plant communities may respond differently to different kinds of water-level regimes. For example, changing the frequency or the timing of water-level fluctuations may produce different effects. We tested this in the present study by comparing regulated sites experiencing four different types of artificial water-level regimes with sites along free-flowing rivers.

The dispersal capacities of species may be important to know in order to predict their responses to regulation of the river's flow and water levels. Many species were lost at the onset of regulation, especially when water levels were raised, leaving the former river margin permanently flooded. In such situations riparian species must recolonize after the onset of regulation. Furthermore, regulated river margins are often subject to strong physical disturbance by the artificial water-level regimes, which may entail frequent local extinctions of riparian plant populations (Nilsson 1981). Thus, for long-term persistence along regulated rivers, some riparian plant species may need to repeatedly establish new populations or to "rescue" declining populations

(Brown and Kodric-Brown 1977, Shmida and Wilson 1985).

Fragmentation of rivers by dams may also affect plant dispersal that is effective along river corridors (Guppy 1891–1893, Schneider and Sharitz 1988, Thébaud and Debussche 1991, Brock 1994). An example of effective dispersal is the rapid spread of exotic plant species along river margins around the world (Richardson et al. 1992, DeFerrari and Naiman 1994, de Waal et al. 1994, Planty-Tabacchi et al. 1996). Plant dispersal by water, or hydrochory, is important in structuring riparian plant communities along rivers (Nilsson et al. 1991b, Johansson and Nilsson 1993, Johansson et al. 1996), but is obstructed by hydroelectric development. Dams are barriers for waterborne diaspores, and the reservoir surfaces between dams tend to be effective traps, since diaspores are likely to be washed ashore by wind and wave action. Furthermore, flood pulses, which are the major events for hydrochory in free-flowing rivers (Schneider and Sharitz 1988, Nilsson et al. 1991b), are reduced or absent. To test whether plants with different dispersal modes respond differently to regulation, we compared the proportions of species with different dispersal traits among the four major types of regulated water-level regime with sites in free-flowing rivers.

The aims of the study were (1) to test the generality and validity of the comparison (Nilsson et al. 1991a) of one free-flowing and one regulated river by comparing other free-flowing and regulated rivers; (2) to test whether river-margin vegetation responds differently to different types of regulation; (3) to test whether species with different mechanisms for dispersal respond differently to river regulation and fragmentation; and (4) to understand which environmental factors are the most important in governing river-margin vegetation along both free-flowing and regulated rivers. Finally, the fundamental differences in river-margin vegetation between free-flowing and regulated boreal rivers are outlined and their implications discussed.

#### STUDY AREAS

Eight rivers in northern Sweden were selected for study. They rise on the border between Norway and Sweden, run southeast for 360–510 km, and empty into the Gulf of Bothnia (Fig. 1), except for the Vindel River which joins the Ume River 35 km from the coast. The rivers are similar in channel length, catchment area, and mean annual discharge (Table 1). The rivers flow from the Scandinavian mountain range through a monadnock plain, to undulating hilly land, flattening out into a narrow coastal plain (Rudberg 1970). The bedrock of the mountain range is complex and partly composed of amphibolites, schists, and sparagmites (Kulling 1953). The remaining area consists of the Baltic shield of Precambrian origin with bedrock composed of predominantly granite and gneiss (Hjelmqvist 1953).

Biogeographically, the rivers run through the boreal

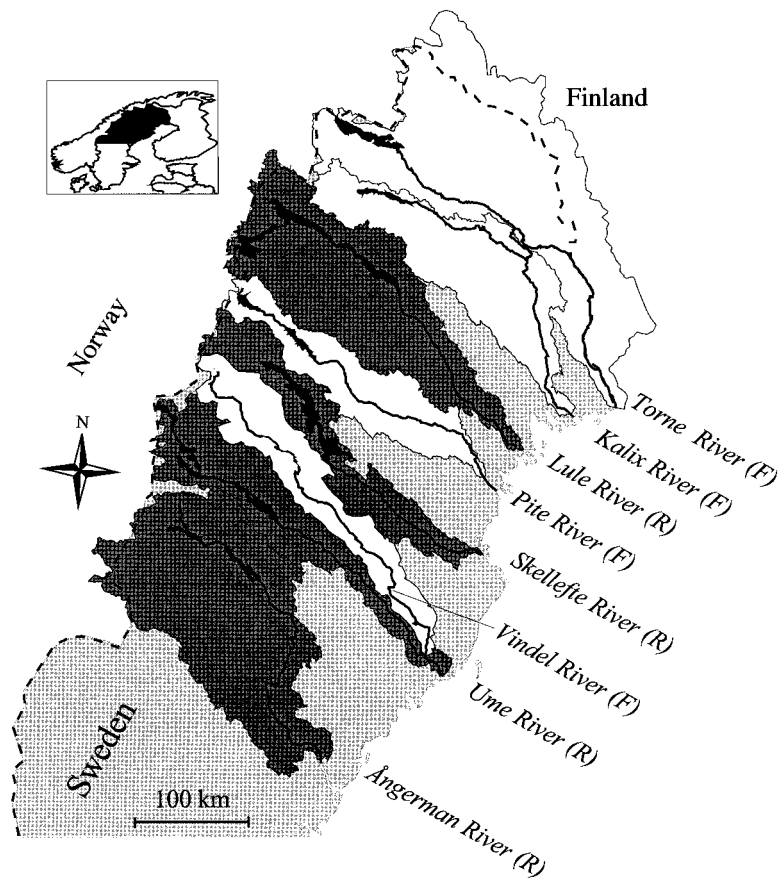


FIG. 1. Map of northern Sweden with the eight studied rivers and their catchments. The catchments of free-flowing rivers (F) are white, those of regulated rivers (R) are dark gray. The land area of Sweden outside these catchments is light gray, with national borders marked by dashed lines. This area corresponds to the black area in the inset map of Scandinavia.

TABLE 1. Hydrological data on the eight Swedish rivers, following Melin and Gihl (1957), except when another source is indicated.

River	Main channel length (km)	Catchment area (km <sup>2</sup> )	Annual discharge at the river mouth (m <sup>3</sup> /s)			Flow regulation (%) <sup>†</sup>	Number of major dams <sup>‡</sup>	
			Mean	Mean minimum	Mean maximum		Main channel	Tributary
Free-flowing rivers								
Torne River	510	30 330 <sup>§</sup>	350	45	2750	0	0	3
Kalix River	450	17 950	290 <sup>  </sup>	33	2890	0	0	0
Pite River	360	11 220	170	20	1170	4	2	2
Vindel River	445	12 650	190 <sup>¶</sup>	15	1660	0	0	1
Regulated rivers								
Lule River	450	25 250	510	52 <sup>#</sup>	2650 <sup>#</sup>	72	9	7
Skellefte River	405	11 600	160	20 <sup>#</sup>	720 <sup>#</sup>	62	15	1
Ume River	455	13 100	230 <sup>¶</sup>	72 <sup>#</sup>	1800 <sup>#</sup>	27	16	4
Ängerman River	440	31 890	490	62 <sup>#</sup>	1970 <sup>#</sup>	43	16	30

<sup>†</sup> Based on live storage, expressed as percentage of virgin mean annual discharge (Dynesius and Nilsson 1994).

<sup>‡</sup> Up to 1991, excluding smaller structures such as dams for mills and timber floating.

<sup>§</sup> Of which 9910 km<sup>2</sup> is common with the Kalix River.

<sup>||</sup> Of which ~90 m<sup>3</sup>/s comes from the Torne River through the Täreändö River, a natural cross-channel connection.

<sup>¶</sup> At the point where the Vindel River joins the Ume River.

<sup>#</sup> Discharge records obtained before hydroelectric exploitation of the rivers.

coniferous zone, with a cold-temperate climate (Walter 1985). The upland vegetation along the rivers ranges from subalpine birch forests dominated by *Betula pubescens* ssp. *tortuosa*, to coniferous forests dominated by *Pinus sylvestris* and *Picea abies*. The annual growing season on non-riparian land (days with a mean temperature exceeding +3°C) ranges from <130 d at the headwaters in the northernmost rivers, to ~170 d at the mouth of the southernmost Ångerman River (Ångström 1974).

Four rivers (Torne, Kalix, Pite and Vindel) are largely free flowing with large seasonal water-level fluctuations (up to 6 m). The annual water-level maximum occurs during the spring or early summer (Fig. 2A) due to snowmelt in the mountains, and delays the development of river-margin vegetation until water levels recede. During this spring flood, ice jams may cause additional floods, especially in the two northernmost Torne and Kalix rivers (Raab and Zachrisson 1984). The mean water levels then recede gradually until the next spring flood, except for a minor, rain-induced increase in the fall. The seasonal flow variations are large: the annual maximum spring flood is typically two orders of magnitude larger than the annual minimum discharge in late winter (Table 1). However, the variation in flow among years is small. Close to the river mouths the coefficients of variation of the maximum annual flows (attained during spring flood) ranged between 7 and 24% for the four rivers during 1937–1975 (Anonymous 1979). Such small variations suggest environmental predictability among years.

Four rivers (Lule, Skellefte, Ume, and Ångerman) are strongly developed for hydroelectric power. The main channels have been transformed by 9–16 dams in each river into chains of consecutive reservoirs and impoundments with very few unimpounded reaches (Table 1). There are also additional dams in the tributaries. Prior to regulation, these rivers exhibited free-flowing water-level fluctuations similar to the remaining rivers. Now they exhibit four major kinds of regulated water-level regime:

1) In the high-capacity storage reservoirs of the upper reaches, the water level is at its lowest in spring and is then raised to reach its maximum in late summer (Fig. 2B). Thus most of the river margins become inundated during the growing season, and most of the margin is barren (Fig. 3B). The water level is subsequently lowered during fall and winter. The water-level fluctuations range from a few to 34.5 m (Sundborg 1977).

2) In the low-capacity, run-of-river impoundments of the middle and lower reaches, the water level exhibits daily or weekly fluctuations between its statutory high and low levels (in most cases 0.5–1 m apart) throughout the year (Fig. 2C). The river margins resemble shorelines in high, headwater lakes in that water-level amplitudes are small and erosion from water flow is unimportant except from the closest down-

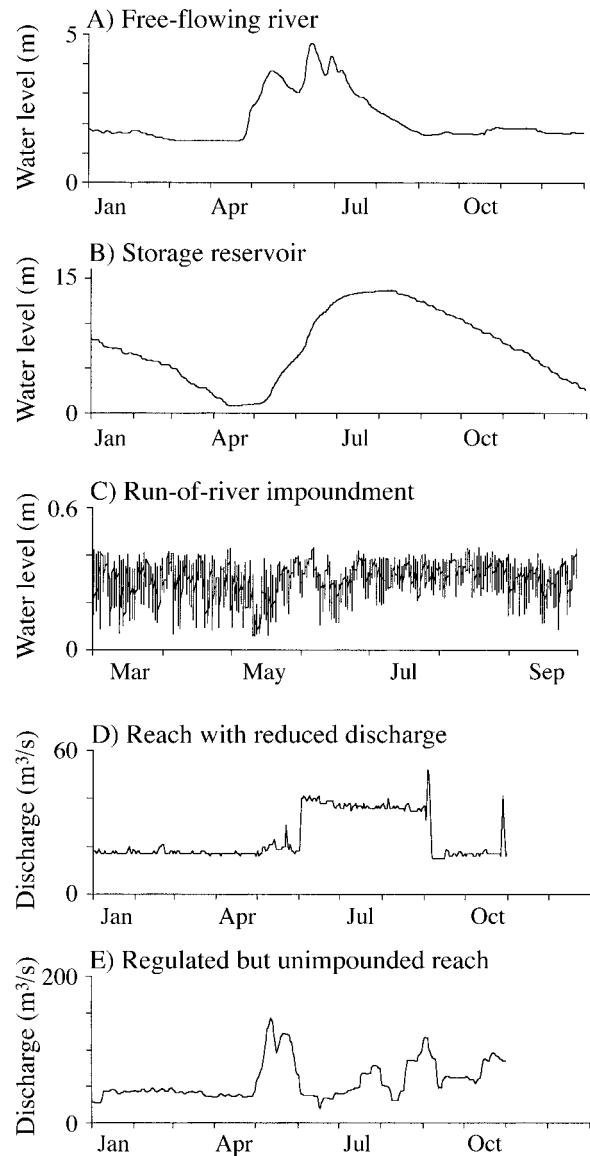


FIG. 2. Hydrographs for (A) a free-flowing river and (B)–(E) the four major types of regulated flow in northern Sweden. Data are from the Swedish Meteorological and Hydrological Institute (Norrköping, Sweden) and Nordkraft Service (Umeå, Sweden).

stream outlets of the power stations, but wave erosion may be strong (Fig. 3C).

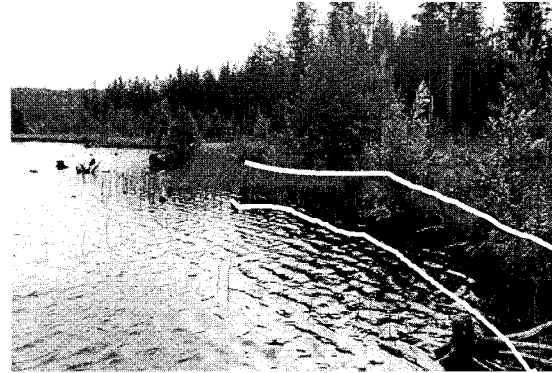
3) In some sections of the rivers, sometimes several kilometers long, the river channel is dry or has very low discharge because of underground passage through tunnels and hydroelectric power stations (Figs. 2D and 3D). These reaches may receive occasional high flows during water release from upstream dams.

4) There are also reaches that are not impounded by a dam downstream, but where flow is affected by upstream dams (Fig. 2E). These reaches maintain their annual discharge but water-level fluctuations are often

A) Free-flowing river



B) Run-of-river impoundment



C) Storage reservoir



D) Reach with reduced discharge



FIG. 3. River-margins experiencing four different kinds of water-level regime. The white lines mark the upper and lower limits of the sampled river-margin area. (A) Free-flowing river. Note the distinct zonation of the river-margin vegetation, going from forest communities at the top, to shrub vegetation, to herbaceous communities, to amphibious species at the bottom. The shrub zone is poorly developed in this particular case due to wave disturbance. (B) Run-of-river impoundment with poor zonation of the river-margin vegetation. Note the stumps in the water from former forest. (C) Storage reservoir during low water level. (D) Reach with reduced flow.

reduced in height, although in many cases with a largely natural rhythm.

All rivers representing the free-flowing stage are not unaffected by dams. The Vindel River joins the regulated Ume River 10 km above a major dam that also regulates the lowermost 10 km of the Vindel River (Table 1). The flow of the Pite River is regulated to a degree of 4 % by three storage reservoirs, and a dam with a hydroelectric power station is situated on the main channel 38 km from the mouth (Table 1). The Torne and Kalix rivers are unaffected by river regulation, except for a few impoundments on the Tengeliö River, a Finnish tributary to the lowermost Torne River. The Torne and Kalix rivers, interconnected by a natural cross-channel, the Tärendö River, form the largest free-flowing river system of Europe outside Russia (Dynesius and Nilsson 1994).

The river-margin vegetation along the free-flowing rivers is distinctly vertically zoned, from forest communities at the top with *Pinus sylvestris* and *Alnus incana* among the dominant tree species, to shrub vegetation of predominantly *Salix* spp., to herbaceous com-

munities with *Carex* spp. and amphibious species such as *Ranunculus reptans* at the bottom (Fig 3A). Plant species richness is generally highest in the riparian forest community (Nilsson 1983). The river margins along the regulated rivers generally lack such a distinctive zonation. The vegetation on the reservoir shorelines (i.e., storage reservoirs and run-of-river impoundments) can be separated into a narrow strip without clear dominants close to the high-water level, and below this a sparse occurrence of amphibious species such as *Ranunculus reptans* and *Subularia aquatica* (Fig. 3B and C). In the run-of-river impoundments, plant species typical of lakes, such as *Carex rostrata* and *Phragmites australis*, have colonized due to small water-level amplitudes and slow water currents. The river-margin flora along all rivers studied is composed of species indigenous to Sweden, i.e., exotics or non-natives are largely absent.

We infer the effects of river regulation by comparing river-margin vegetation along the free-flowing and the regulated rivers, thus assuming that the river-margin vegetation was similar between the two groups of river

prior to regulation. The validity of this assumption cannot be tested directly due to lack of quantitative pre-regulation data, but is supported by historical documentation. The most important of this material are botanical surveys made during the planning of the hydroelectric schemes (Lundqvist 1970, Sjors 1973), showing that preregulation characteristics such as plant zonation and species richness were similar to that of the remaining free-flowing rivers. Species composition differed somewhat geographically, but was highly similar between adjacent rivers (Lundqvist 1970, Sjors 1973). Other documentary material includes photos (examples in Grelsson and Nilsson [1982]), and remnants of preregulation river-margin vegetation, now left unflooded along regulated rivers (Grelsson and Nilsson 1980). River systems with high percentages of lakes and much of the altitudinal range concentrated into steep rapids were chosen first for regulation, but differences between rivers were small and there are no indications that those differences affected plant species richness.

## METHODS

### *Vegetation*

The entire main channel of each river was divided into equally long sections, with one study site located in the middle of each section. The number of sites differed among rivers, because data were collected on different occasions. We investigated the Torne River in 1985, the Kalix River in 1986, the Vindel and Ume Rivers in 1988, and the remaining rivers in 1991. Because each study site covered a large area (see next paragraph) and >90% of the river-margin plant species in the area are perennial, between-year differences in species composition are small and considered unimportant. We sampled 46 sites in the Torne River, 37 sites in the Kalix River, 25 sites in each of the Vindel and Ume Rivers, and 10 sites in each of the remaining rivers. Thus, the distance between study sites varied among rivers, from 10 km in the Torne and Kalix Rivers to 45 km in the Lule River. Study sites were always located on the northern side of the rivers, except from one site in the Lule River and two sites in the Pite River, where absence of roads made this side difficult to access.

Each site in the free-flowing rivers encompassed a 200-m-long stretch of riverbank or lakeshore, spanning the entire area between the summer low-water and spring high-water levels, attained at least once every two years. In free-flowing rivers, this area is available for plant growth unless the substrate is too coarse grained. We sampled an analogous area also in the regulated rivers. In the storage reservoirs, this was identical to the area between the statutory damming and drawdown levels, whereas in most run-of-river impoundments it encompassed the uppermost 0.5–1 m vertical interval of the shoreline, i.e., the zone between

the damming level and the level of summer drawdown. If all parts of this area were not available for plant growth in the regulated rivers, this would indicate a major environmental change. To maximize the likelihood of encountering all species present at the site, we sampled one large area at each site rather than many small plots. In free-flowing rivers, the limit of the summer low-water level was defined as the lower end of continuous *Carex* vegetation, and the high-water limit was defined as the lower boundary of a continuous *Vaccinium myrtillus* carpet (Wassén 1966, Nilsson 1979). The presence of debris deposited by the spring flood often helped to define the upper limit of the river margin.

At each site we recorded all vascular plant species present. The definition of a "species" follows the taxonomy in Krok and Almquist (1984). In the following cases two or more species were treated as one taxon: *Alchemilla vulgaris* coll., *Callitriche* spp., *Carex juncella* + *C. nigra*, *Dactylorhiza maculata* + *D. fuchsii*, *Equisetum variegatum* + *E. scirpoides*, *Euphrasia frigida* + *E. stricta*, *Hieracium* spp., *Hierochloë hirta* + *H. odorata*, *Luzula multiflorum* + *L. sudetica*, *Poa nemoralis* + *P. palustris*, *Rhinanthus groenlandicus* + *R. minor*, *Sagittaria natans* + *S. sagittifolia*, *Salix borealis* + *S. myrsinifolia* + *S. phyllicifolia*, *Salix starkeana* + *S. xerophila*, *Sparganium* spp., *Taraxacum* spp., and *Thalictrum flavum* + *T. simplex*. We also estimated the percentage cover of trees + shrubs (individuals of woody species >0.25 m) and dwarf shrubs (<0.25 m) + herbs. To reduce the error almost always present in vegetation analyses (Lepš and Hadincová 1992) every site was analyzed individually by two persons and results were combined (Nilsson 1992).

### *Environment*

At each site we determined the width and height of the river margin, the number of substrates, and the percentage cover of each substrate, using nine grain sizes (the Wentworth groups: clay, silt, sand, gravel, pebbles, cobbles, and boulders [Chorley et al. 1984], supplemented by bedrock and peat), width of the river, mean annual discharge, catchment area, and length of the growing season. Recording the cover of each substrate, albeit not very precise, gives a good representation of the overall substrate composition of deeper soil at the site (R. Jansson, *personal observations*). We calculated substrate fineness by weighing log<sub>2</sub>-transformed values of mean particle size by percentage composition of the river-margin substrate (Wright et al. 1984, Nilsson et al. 1989). Width of the river margin was measured at five locations 50 m apart, as the distance between summer low-water level and spring high-water level. Height of the river margin was measured as the vertical distance between these two levels, using a rod and level. We calculated the area of each site as the mean of the five width measurements multiplied by the length of the site (always 200 m). Width

of the river and catchment area were measured on maps. Mean annual discharge was estimated for each site using data presented by the Swedish Meteorological and Hydrological Institute (Anonymous 1979), and length of the growing season was estimated from Ångström (1974).

#### Data analysis

To test whether different species respond differently to regulation, we classified the species into functional groups, each group sharing a specific trait. Equivalent terms are “guilds” (Root 1967), “strategies” (Grime 1979, Tilman 1988) or “life-history types” (van der Valk 1981). We made four different classifications of the flora: (1) *morphology*: trees + shrubs, dwarf shrubs, forbs + ferns, and graminoids; (2) *naturalness*: natural vs. ruderal species (following Lid 1987), where ruderal species represent species mainly occurring in human-made habitats, e.g., wasteland, cultivated land, and meadows; (3) *location*: riparian and terrestrial vs. aquatic species (following Nilsson 1983); and (4) *life cycle*: perennial vs. annual + biennial species (following Lid 1987).

We also classified species according to seven dispersal mechanisms: dispersal by water (hydrochory), wind (anemochory), vertebrates (zoochory: epizoic or endozoic), ants (myrmecochory), no mechanisms for dispersal, and vegetative dispersal. All classifications include the entire flora, except for hydrochory, where data were available for 234 of 508 species. Species with seeds and fruits that float for 2 d or more were defined as “long-floaters”; the remaining species were “short-floaters” (data from Romell 1938, Danvind and Nilsson 1997, and E. Andersson, *unpublished manuscript*). When several data were available, we used the mean floating time. However, most of the data on floating capacity come from a compilation of experimental studies by Romell (1938). The general method in these studies was to place a number of diaspores in water and to record maximum floating time when the last diaspore had sunk. Romell (1938) reports the longest floating time in classes (hours, days, weeks etc.), often as a range (e.g., days to months), and we consistently used the average of this range. Many species float well without having distinct morphological adaptations for water dispersal. Therefore, buoyancy records describe the ability of being water-dispersed more accurately than morphological criteria. The germinability of the buoyant diaspores in the buoyancy tests was generally high, and in some cases even increased compared to diaspores that were not tested (E. Andersson, *unpublished manuscript*).

Anemochores (e.g., *Betula* spp., most Asteraceae spp.) and zoochores (endozoic dispersal: e.g., *Vaccinium* spp., *Sorbus* spp.; epizoic dispersal: e.g., many Poaceae spp.) and myrmecochores (e.g., *Viola* spp. and *Luzula* spp.) were classified following a scheme of Willson et al. (1990). The remaining species were con-

sidered as lacking mechanisms for dispersal. Species with ballistic dispersal were included in this group, because seeds released by this mechanism usually travel very short distances (e.g., van der Pijl 1982). We also judged whether the species have more or less differentiated vegetative structures that can be detached and dispersed (in this case mainly by water). Vegetative dispersal is common in most aquatic and many riverine plants (e.g., *Ranunculus* spp. and *Salix* spp.; Bartley and Spence 1987, Cook 1987).

For each site, we calculated the number of species of the entire flora and of the different functional groups. Although study sites were always 200 m long, sample area varied among sites due to variation in height and slope of the river margins. To correct for differences in species richness due to variation in sample area, we calculated species density by dividing the number of species for each site by the  $\log_{10}$  of the area sampled (Whittaker 1972, Connor and McCoy 1979). Values were then standardized by multiplying with the  $\log_{10}$  of the mean sample area for all rivers (4648.15 m<sup>2</sup>).

*Comparison of five rivers.*—To test the generality of a previous comparison of the Vindel and Ume rivers (Nilsson et al. 1991a), we compared (1) the free-flowing Torne and Kalix rivers with the regulated Lule River, and (2) the free-flowing Pite River with the regulated Skellefte River. The rivers in each of these two sets of rivers are adjacent with similar climates (Lundqvist 1953–1971), geology (Hjelmqvist 1953), and regional species pools (Mossberg et al. 1992). Although there are some between-river differences in the size of the catchment area, the percentage of lakes, and the features of the river channel, the rivers in each set are equally long and exhibited similar water-level regimes prior to regulation, including spring flooding and low winter flows (Table 1). The regulated Ångerman River was not compared with any river, because it is geographically separated from the other five rivers (Fig. 1), and contains some species of mainly southern distribution that are absent further north.

To test for overall differences we compared variables describing the vegetation and environment between the Torne, Kalix and Lule rivers, using the Kruskal-Wallis test. We also compared the Pite and Skellefte rivers using the Mann-Whitney *U* test. In addition, to test for a general pattern, we compared regulated vs. free-flowing sites in the five rivers, using the Mann-Whitney *U* test. In these analyses 14 variables described the vegetation: the total number of species and species density per site, the species density of the various functional groups, classified by morphology, naturalness, location and life cycle, and the percentage cover of trees + shrubs, and herbs + dwarf shrubs. The physical factors were described by the length of the growing season, mean annual discharge, width of the river, height and width of the river margin, number of substrates, and substrate fineness.

*Type of regulation.*—To test if the effects of river



TABLE 2. Comparison of environmental and vegetation-cover variables between (1) the free-flowing Torne and Kalix rivers and the regulated Lule River, and (2) the free-flowing Pite River and the regulated Skellefte River ( $n$  = no. of river-margin sites). The last column of  $P$  values refers to a previous comparison of the free-flowing Vindel and the regulated Ume rivers (Nilsson et al. 1991a).

Variable	Comparison of three rivers						$P$ †
	Torne River ( $n$ = 46; free-flowing)		Kalix River ( $n$ = 37; free-flowing)		Lule River ( $n$ = 10; regulated)		
	Mean	1 SE	Mean	1 SE	Mean	1 SE	
<b>Environmental factors</b>							
Growing season (d)	144	1.5	144	1.9	146	4.1	0.77
Discharge (m <sup>3</sup> /s)	183 <sup>a</sup>	19.1	137 <sup>a</sup>	15.5	319 <sup>b</sup>	42.6	<b>0.0021</b>
Width of river (m)	1080 <sup>a</sup>	237	490 <sup>a</sup>	93	1360 <sup>a</sup>	529	0.039§
Height of river margin (m)	1.9	0.16	2.1	0.16	4.6	2.85	0.75
Width of river margin (m)	24	4.3	20	3.0	88	68.3	0.99
Substrate fineness	1.0 <sup>ab</sup>	1.01	3.2 <sup>a</sup>	0.76	-2.7 <sup>b</sup>	2.29	0.034§
Number of substrates	3.1 <sup>a</sup>	0.16	4.6 <sup>b</sup>	0.28	3.7 <sup>ab</sup>	0.47	<b>0.0001</b>
<b>Vegetation cover</b>							
Herbs + dwarf shrubs (%)	66 <sup>a</sup>	3.9	...	...	11 <sup>b</sup>	7.2	< <b>0.0001</b>
Trees + shrubs (%)	...	...	...	...	14	8.3	...

Notes: Means with different lowercase superscript letters are significantly different at  $P < 0.05$  according to nonparametric multiple comparisons with unequal sample sizes (Zar 1996). Ellipses indicate lack of data. Significant ( $P < 0.05$ ) differences are boldfaced.

† Kruskal-Wallis test.

‡ Mann-Whitney  $U$  test, two-tailed probability.

§ Not significant after Bonferroni correction, using a sequential procedure (Holm 1979) of the Dunn-Šidák method (Sokal and Rohlf 1995).

regulation varied depending on the kind of regulated water-level regime, we compared variables describing the vegetation and environment between the four types of regulation identified above (storage reservoirs, run-of-river impoundments, reaches with reduced discharge, and unimpounded but regulated reaches) with sites in the free-flowing rivers, using one-way ANOVA or the Kruskal-Wallis test. In these analyses, we included all study sites from all eight rivers, giving a total of 173 sites. Four variables described the vegetation: the total number of species and species density per site, and the percentage cover of trees + shrubs, and herbs + dwarf shrubs. Cover values were arcsine transformed and species density was squared prior to analysis. The physical factors were described by five variables: width of the river, height and width of the river margin, number of substrates, and substrate fineness.

In these and the following analyses we assume that sites were independent, although there were several sites in each river. When free-flowing and regulated rivers were treated separately, river affiliation was a poor predictor of species numbers. It did not enter the regression models to explain the variation in species numbers ( $P > 0.05$ ), but variables describing substrate composition and river-margin height were significant ( $P < 0.05$ ). This suggests that local site conditions were more important in determining species composition than some spatial dependency among sites within a river.

*Dispersal traits.*—We tested whether species with different mechanisms for dispersal responded differ-

ently to river regulation. We did this by comparing the proportion of species per site, grouped after mechanisms for dispersal, between the free-flowing rivers and the four major types of regulated water-level regime, using one-way ANOVA. In these analyses, we included all study sites from all eight rivers, giving a total of 173 sites.

To ensure that the “experiment-wise” significance level always was  $\alpha = 0.05$  irrespective of the number of statistical tests, we always adjusted the Type I error rate using sequential Bonferroni tests, i.e., a sequential procedure (Holm 1979) of the Dunn-Šidák method (Sokal and Rohlf 1995). We also calculated the statistical power of the tests to address the risk of committing Type II errors.

*Relationship between vegetation and environment.*—In the following analyses, we used data from all eight rivers, but to give equal weight to all rivers we used only 10 sites from each river, i.e., a total of 80 sites, 40 from the free-flowing and 40 from the regulated rivers. In cases where there were >10 sites from a river, we chose subsets of sites to ensure that selected sites lay at equal distances along the entire river.

We tested how much of the variation in the variables describing river-margin vegetation could be explained by the environment. Because several of the environmental variables were correlated, we used partial least-squares (PLS) regression (Geladi and Kowalski 1986, Martens and Naes 1989). In PLS regression the problem of correlation among the dependent  $x$  variables is overcome by projecting the observed  $x$  variables onto a few “latent” variables (components), rather than by

TABLE 2. Extended.

Comparison of two rivers					
Pite River ( <i>n</i> = 10; free-flowing)		Skellefte River ( <i>n</i> = 10; regulated)		<i>P</i> ‡	Vindel vs. Ume rivers <i>P</i> ‡
Mean	1 SE	Mean	1 SE		
146	3.8	144	2.6	0.88	0.81
107	11.7	107	13.6	0.71	0.071
570	199	600	251	0.49	0.37
1.2	0.13	3.2	1.49	0.14	0.29
9	2.3	16	5.0	0.26	0.14
-0.8	1.88	-6.2	1.54	0.028‡	<b>0.0021</b>
3.5	0.56	4.7	0.40	0.16	0.052
25	4.2	13	6.2	0.058	<b>&lt;0.0001</b>
27	5.2	9	4.0	0.0075‡	<b>&lt;0.0001</b>

selecting among variables as in stepwise multiple regression. These latent variables or components are then used as independent variables in the regressions. The components are estimated consecutively and the significance of each component in the model is determined by cross-validation, i.e., parameters are estimated on one part of the data matrix, and the prediction is tested on another part (Wold 1978). The contribution of each observed *x* variable in a component is given by its variable loading. A variable with little influence on the model is close to the perpendicular of the PLS component and gets a loading close to 0. A positive loading means that the variable is positively correlated with *y* and vice versa for a negative loading. Prior to the PLS modeling, all variables were standardized to have a mean of 0 and a standard deviation of 1, by subtracting the mean from each variable and multiplying with the inverse of the standard deviation. This procedure is recommended when no a priori assumption is made on the relative importance of the observed variables (Martens and Naes 1989).

In the PLS modeling, we used 15 variables describing the environment: length of the growing season (in days), latitude, catchment area (in square kilometers), altitude (in meters above sea level), width of the river (in meters), height and width of the river margin (in meters), the percentage cover values of peat, clay + silt, sand + gravel, stones, and bedrock, plus three dummy variables. The dummy variables were any kind of regulated water flow vs. natural water flow, any kind of reservoir (i.e., storage reservoirs and run-of-river impoundments) vs. non-reservoir, and the preregulation position of the river margin. Width and height of the river margins and the substrate cover values were  $\log_{10}$ -transformed prior to the analysis to better fit a normal distribution. In the PLS regressions, data from all eight rivers were combined. We examined the data for non-linearities and outliers, and the influence of outliers

were examined by removing them to test whether patterns changed. To enable comparisons with the previous study (Nilsson et al. 1991a), we also performed the regressions excluding data from the Ume and Vindel rivers.

In all statistical analyses we used the SPSS software package (Norusis 1993), except for the PLS regressions, which were made using the computer program SIRIUS (version 2.3, Pattern Recognition Systems A/S, 5015 Bergen, Norway). The power analyses were made using the computer program PASS 6.0 (NCSS, Kaysville, Utah, USA).

## RESULTS

First, we present the results from the comparisons of the Torne, Kalix, and Lule rivers, and the Pite and Skellefte rivers. Second, we present the results from the comparison of four different regulated-water-level regimes with sites in the free-flowing rivers, and third the results from similar comparisons of species with different dispersal mechanisms. Fourth, we present our analyses of the relationships between the river-margin vegetation and the environment. We then compare the results with those of Nilsson et al. (1991a).

### Comparison of five rivers

The regulated sites had more coarse-grained soils than the sites along free-flowing rivers ( $-4.4 \pm 1.40$  vs.  $1.7 \pm 0.63$  [mean  $\pm$  1 SE],  $P = 0.00011$ , Mann-Whitney *U* test), but the other environmental variables did not differ significantly ( $P > 0.05$ ). The percentage cover of both herbs + dwarf shrubs ( $14 \pm 2.9$  vs.  $55 \pm 3.0$ ) and of trees + shrubs ( $12 \pm 5.2$  vs.  $27 \pm 5.2$ ) were lower on the regulated sites ( $P < 0.0001$ ). Both the number of species per site ( $63 \pm 6.9$  vs.  $91 \pm 1.7$ ) and species density ( $55 \pm 5.3$  vs.  $84 \pm 1.7$ ) were lower in the regulated than in free-flowing rivers ( $P < 0.0001$ ).

The Torne, Kalix, and Lule rivers differed in some of the environmental variables. The Lule River had higher mean annual discharge than the other two rivers ( $P = 0.0021$ , Kruskal-Wallis test, Table 2). The Kalix River had more river-margin substrates than the Torne River ( $P = 0.0001$ , Table 2). The percentage cover of herbs and dwarf shrubs was higher in the Torne than in the Lule River ( $P < 0.0001$ , Table 2). On average, herbs and dwarf shrubs covered 66% of the river margins along the Torne River, but only 11% of the river margins along the Lule River (data from the Kalix River are missing, Table 2).

The total number of species and species density per site were higher in the free-flowing Torne and Kalix rivers than in the regulated Lule River, ( $P = 0.0002$  and  $P = 0.0015$ , respectively; Kruskal-Wallis test, Table 3). The species densities of functional groups of species were higher in the Torne and Kalix rivers ( $P < 0.05$ ), except for tree and shrub species, ruderal spe-

TABLE 3. Comparison of the number of species per site for all species and for different functional groups between (1) the free-flowing Torne and Kalix rivers and the regulated Lule River, and (2) the free-flowing Pite River and the regulated Skellefte River, ( $n$  = no. of river-margin sites). The last column of  $P$  values refers to a previous comparison of the free-flowing Vindel and the regulated Ume rivers (Nilsson et al. 1991a).

Variable	Comparison of three rivers						$P$ †
	Torne River ( $n$ = 46; free-flowing)		Kalix River ( $n$ = 37; free-flowing)		Lule River ( $n$ = 10; regulated)		
	Mean	1 SE	Mean	1 SE	Mean	1 SE	
Species richness of entire flora							
Number of species	85.0 <sup>a</sup>	2.34	86.4 <sup>a</sup>	2.11	55.0 <sup>b</sup>	6.61	<b>0.0002</b>
Species density	91.5 <sup>a</sup>	2.13	94.3 <sup>a</sup>	2.51	64.2 <sup>b</sup>	10.3	<b>0.0015</b>
Morphology							
Trees + shrubs	8.6	0.25	9.4	0.38	9.8	2.00	0.37
Dwarf shrubs	7.3 <sup>a</sup>	0.49	7.7 <sup>a</sup>	0.51	4.3 <sup>b</sup>	0.79	<b>0.014</b>
Forbs + ferns	49.1 <sup>a</sup>	1.59	49.2 <sup>a</sup>	1.51	30.5 <sup>b</sup>	5.50	<b>0.0019</b>
Graminoids	26.6 <sup>a</sup>	0.87	28.0 <sup>a</sup>	0.93	19.5 <sup>b</sup>	2.97	<b>0.010</b>
Naturalness							
Ruderal species	4.7	0.81	4.1	0.86	2.7	1.01	0.35
Natural species	86.3 <sup>a</sup>	2.00	89.5 <sup>a</sup>	2.50	61.4 <sup>b</sup>	9.85	<b>0.0016</b>
Location							
Aquatic species	9.2	0.82	8.0	0.75	6.1	1.92	0.17
Riparian + terrestrial spp.	81.9 <sup>a</sup>	2.04	85.2 <sup>a</sup>	2.47	57.9 <sup>b</sup>	9.41	<b>0.0008</b>
Life cycle							
Annuals + biennials	6.2 <sup>a</sup>	0.42	6.4 <sup>a</sup>	0.48	3.1 <sup>b</sup>	0.87	<b>0.0060</b>
Perennials	84.8 <sup>a</sup>	1.92	87.4 <sup>a</sup>	2.38	60.7 <sup>b</sup>	9.81	<b>0.0014</b>

Notes: Means with different lowercase superscript letters are significantly different at  $P < 0.05$  according to nonparametric multiple comparisons with unequal sample sizes (Zar 1996). Significant ( $P < 0.05$ ) differences are boldfaced.

† Kruskal-Wallis test, two-tailed probability.

‡ Mann-Whitney  $U$  test, two-tailed probability.

cies, and aquatic species that were not significantly different between rivers ( $P > 0.05$ , Table 3).

The percentage cover of trees and shrubs was higher and the river-margin substrates were more fine grained in the free-flowing Pite River than in the regulated Skellefte River, but differences were not significant after Bonferroni correction ( $P > 0.05$ , Mann-Whitney  $U$  test; Table 2). Neither the number of species, nor species densities per site, differed between the Pite and the Skellefte rivers ( $P > 0.05$ , Table 3). Furthermore, species density did not differ for any of the functional groups ( $P > 0.05$ , Table 3). However, the statistical power of these tests was too low to conclude that there were no differences (power  $< 0.44$ ).

#### Type of regulation

All four types of regulated water-level regimes had more coarse-grained river-margin soils compared to the free-flowing rivers ( $P < 0.0001$ , Kruskal-Wallis test, Table 4), but the number of substrates did not differ significantly among flow regimes ( $P > 0.05$ ).

The percentage cover of trees and shrubs was highest on river-margins along free-flowing rivers, lower along run-of-river impoundments, and lowest along storage reservoirs ( $P < 0.0001$ , one-way ANOVA, Table 4). The regulated but unimpounded reaches had lower percentage cover of trees and shrubs than free-flowing rivers, but did not differ significantly from any of the other types of regulation ( $P > 0.05$ , power  $< 0.46$ ).

Reaches with reduced discharge did not differ significantly in cover from any of the other flow regimes, but the statistical powers of the comparisons were low (power  $< 0.66$ ).

Regulated margins (including all four types of regulated flow) had lower percentage cover of herbs and dwarf shrubs than the free-flowing rivers ( $P < 0.0001$ , one-way ANOVA, Table 4), but did not differ significantly among the different types of regulation ( $P > 0.05$ ). However, the statistical power was too low in all comparisons to conclude that such differences do not exist (power  $< 0.51$ ), except for between storage reservoirs and run-of-river impoundments (power = 0.93).

The number of species per site was lower on regulated river margins (including all types of regulated flow) than on free-flowing river-margins, except for the unimpounded reaches ( $P < 0.0001$ , one-way ANOVA, Table 4), but did not differ among types of regulation ( $P > 0.05$ , power  $< 0.20$ ). When species-density values were used, the differences between the free-flowing rivers vs. storage reservoirs and run-of-river impoundments remained significant ( $P < 0.0001$ , one-way ANOVA, Table 4), but not between free-flowing rivers and reaches with reduced discharge ( $P > 0.05$ ). However, statistical power was too low to conclude that they do not differ in species density (power = 0.29). The margins along regulated but unimpounded reaches had significantly higher species density than storage

TABLE 3. Extended.

Comparison of two rivers					Vindel vs. Ume Rivers $P_{\ddagger}^{\dagger}$
Pite River ( $n = 10$ ; free-flowing)		Skellefte River ( $n = 10$ ; regulated)		$P_{\ddagger}^{\dagger}$	
Mean	1 SE	Mean	1 SE		
65.7	5.49	54.2	8.56	0.60	<b>0.0001</b>
79.7	7.13	62.0	9.57	0.20	<b>0.0016</b>
13.0	1.48	9.1	1.52	0.059	<b>0.0001</b>
8.2	1.14	6.5	1.06	0.21	<b>0.0001</b>
36.0	4.67	25.5	4.72	0.17	<b>0.0026</b>
22.5	2.57	21.0	3.28	0.82	<b>0.028</b>
1.8	1.42	0.8	0.42	0.84	0.30
77.6	6.88	61.1	9.55	0.26	<b>0.0022</b>
4.1	0.91	6.2	1.78	0.34	0.36
75.0	6.92	55.5	8.31	0.13	<b>0.0009</b>
2.0	0.78	2.3	0.59	0.60	0.90
77.5	6.73	59.5	9.22	0.20	<b>0.0011</b>

reservoirs and run-of-river impoundments ( $P < 0.05$ ), but did not differ significantly from free-flowing rivers and reaches with reduced discharge ( $P > 0.05$ , power  $< 0.29$ ). Species richness (the number of species and species density per site) did not vary linearly with the number of years regulation had been in operation for any of the types of regulation ( $P > 0.05$ , linear least-squares regression).

TABLE 4. Comparison of environmental and vegetation variables between free-flowing rivers and four major types of regulated flow.

Variable	Free-flowing rivers ( $n = 118$ )		Storage reservoirs ( $n = 15$ )		Run-of-river impound- ments ( $n = 24$ )		Reaches with reduced discharge ( $n = 7$ )		Regulated but unimpounded reaches ( $n = 9$ )		$P$
	Mean	1 SE	Mean	1 SE	Mean	1 SE	Mean	1 SE	Mean	1 SE	
Substrate fineness	1.8 <sup>a</sup>	0.53	<b>-3.9<sup>bc</sup></b>	<b>1.29</b>	0.8 <sup>ab</sup>	1.17	<b>-7.7<sup>c</sup></b>	<b>1.10</b>	<b>-5.0<sup>bc</sup></b>	<b>1.56</b>	<b>&lt;0.0001<sup>†</sup></b>
Number of substrates	3.7	0.15	4.3	0.32	3.9	0.25	4.6	0.69	5.4	0.56	0.023 <sup>†,‡</sup>
Tree + shrub cover (%)§	39 <sup>a</sup>	4.0	<b>0.3<sup>b</sup></b>	<b>0.15</b>	<b>19<sup>c</sup></b>	<b>5.3</b>	14 <sup>abc</sup>	5.0	<b>16<sup>bc</sup></b>	<b>7.0</b>	<b>&lt;0.0001  </b>
Herb + dwarf shrub cover (%)¶	55 <sup>a</sup>	3.0	<b>1.1<sup>b</sup></b>	<b>0.39</b>	<b>18<sup>b</sup></b>	<b>4.53</b>	<b>19<sup>b</sup></b>	<b>8.1</b>	<b>24<sup>b</sup></b>	<b>9.2</b>	<b>&lt;0.0001  </b>
Number of species	86.6 <sup>a</sup>	1.56	<b>57.6<sup>b</sup></b>	<b>9.23</b>	<b>67.0<sup>b</sup></b>	<b>4.32</b>	<b>60.0<sup>b</sup></b>	<b>11.59</b>	76.2 <sup>ab</sup>	8.34	<b>&lt;0.0001  </b>
Species density	86.2 <sup>a</sup>	1.37	<b>50.0<sup>b</sup></b>	<b>8.34</b>	<b>71.4<sup>b</sup></b>	<b>4.00</b>	65.2 <sup>ab</sup>	14.07	85.4 <sup>a</sup>	9.48	<b>&lt;0.0001  </b>

Notes: Data are from four free-flowing and four regulated Swedish rivers;  $n$  = no. of river-margin sites. Values differing significantly ( $P < 0.05$ ) from free-flowing rivers and significant  $P$  values ( $P < 0.05$ ) are boldfaced. Means with different lowercase superscript letters are significantly different ( $P < 0.05$ ) according to nonparametric multiple comparisons with unequal sample sizes (Kruskal-Wallis tests; Zar 1996) and Bonferroni multiple-comparison tests (one-way ANOVAs).

<sup>†</sup> Kruskal-Wallis test, two-tailed probability.

<sup>‡</sup> Not significant after Bonferroni correction, using a sequential procedure (Holm 1979) of the Dunn-Šidák method (Sokal and Rohlf 1995).

§ In the free-flowing rivers,  $n = 35$ .

|| One-way ANOVA, two-tailed probability.

¶ In the free-flowing rivers,  $n = 80$ .

### Dispersal traits

Compared to the free-flowing rivers, the proportion of wind-dispersed species was higher for all types of regulated flow regime, except for run-of-river impoundments ( $P < 0.0001$ , one-way ANOVA, Table 5). These increases were offset by lower proportions of species with no special devices for dispersal along storage reservoirs and reaches with reduced discharge ( $P < 0.0001$ ). Compared to the free-flowing rivers, the proportion of species with endozoic dispersal increased along storage reservoirs and decreased along regulated but unimpounded reaches ( $P < 0.0001$ ). The run-of-river impoundments had higher proportions of species with long-floating diaspores and species with vegetative dispersal compared to the free-flowing rivers ( $P < 0.0001$ , one-way ANOVA, Table 5). The different mechanisms for dispersal were not positively correlated ( $P > 0.05$ , Spearman's coefficient of rank correlation).

### Relationships between vegetation and environment

There were significant correlations between environmental variables used in the partial least-squares modeling ( $P < 0.05$ , Pearson product-moment correlations, Table 6). The length of the growing season, catchment area, and altitude were significantly correlated. The length of the growing season and catchment area decreased with increasing altitude ( $r > -0.83$ ), and the length of the growing season increased with increasing catchment area ( $r = 0.76$ ). Furthermore, the occurrence of clay and silt in the river-margin soils increased with increasing length of the growing season and decreasing altitude ( $r > |0.38|$ ), reflecting that river valleys are more sediment laden toward the coast. The percentage cover of clay and silt in the river-margin

TABLE 5. The proportion of species per site among species groups with different mechanisms for dispersal, compared between free-flowing rivers and four major types of regulated flow.

Diaspore characteristic	Free-flowing rivers (n = 118)		Storage reservoirs (n = 15)		Run-of-river impoundments (n = 24)		Reaches with reduced discharge (n = 7)		Regulated but unimpounded reaches (n = 9)		P†
	Mean	1 SE	Mean	1 SE	Mean	1 SE	Mean	1 SE	Mean	1 SE	
Floating time											
Short floating (<2 d)	20.4 <sup>ab</sup>	0.43	18.2 <sup>ab</sup>	1.11	19.3 <sup>ab</sup>	0.83	15.5 <sup>a</sup>	2.93	22.5 <sup>b</sup>	1.56	<b>0.016</b>
Long floating (≥2 d)	42.8 <sup>a</sup>	0.38	44.3 <sup>ab</sup>	2.29	<b>48.5<sup>b</sup></b>	<b>1.23</b>	44.9 <sup>ab</sup>	2.08	45.4 <sup>ab</sup>	1.25	<b>&lt;0.0001</b>
Wind dispersal	28.1 <sup>a</sup>	0.35	<b>35.8<sup>b</sup></b>	<b>1.59</b>	30.4 <sup>ac</sup>	1.06	<b>36.3<sup>b</sup></b>	<b>3.55</b>	<b>34.1<sup>bc</sup></b>	<b>1.13</b>	<b>&lt;0.0001</b>
Endozoic dispersal	10.5 <sup>a</sup>	0.26	<b>13.1<sup>b</sup></b>	<b>1.14</b>	9.6 <sup>ac</sup>	0.81	11.9 <sup>ab</sup>	1.22	<b>6.4<sup>c</sup></b>	<b>1.15</b>	<b>&lt;0.0001</b>
Epizoic dispersal	17.2	0.21	18.3	0.99	16.5	0.62	18.5	1.82	18.2	1.32	0.18
Ant dispersal	5.2	0.18	4.6	0.58	4.6	0.53	3.2	1.00	5.3	0.57	0.11
Vegetative dispersal	23.1 <sup>a</sup>	0.49	21.9 <sup>a</sup>	1.71	<b>29.1<sup>b</sup></b>	<b>1.79</b>	26.7 <sup>ab</sup>	2.69	21.0 <sup>a</sup>	2.05	<b>0.00012</b>
No special device for dispersal	41.6 <sup>a</sup>	0.46	<b>31.2<sup>b</sup></b>	<b>2.03</b>	41.4 <sup>ac</sup>	1.29	<b>33.0<sup>bd</sup></b>	<b>3.70</b>	38.7 <sup>acd</sup>	1.64	<b>&lt;0.0001</b>

Notes: Data are from four free-flowing and four regulated Swedish rivers; n = no. of river-margin sites. Values differing significantly (P < 0.05) from free-flowing rivers and significant P values (P < 0.05) are boldfaced. Means with different lowercase superscript letters are significantly different (P < 0.05) according to Bonferroni multiple-comparison tests.

† One-way ANOVA, two-tailed probability.

soil was negatively correlated with the cover of stones (r = -0.49). Furthermore, the height and width of the river margin were significantly correlated (r = 0.86), and both increased with increasing width of the river (r > 0.43). Variables describing regulated-flow regimes (i.e., any kind of regulated water flow vs. natural water flow, any kind of reservoir vs. non-reservoir sites, and preregulation positions of the river margins) were all interrelated (r > 0.67). Furthermore, the occurrence of regulated flows decreased with latitude (r = 0.42), because the position of regulated vs. free-flowing rivers was biased (Fig. 1).

Partial least-squares (PLS) regression generated sta-

tistically significant (P < 0.05) models for all dependent variables describing species richness and percentage cover of the river-margin vegetation in the eight rivers (Table 7). In all models, only the first PLS component was significant (P < 0.05), as determined by cross-validation (Wold 1978). Using a set of 15 environmental factors as predictor variables, the models explained 28–50% of the variation in the dependent variables. Regional factors, as well as local, river-margin factors were important to explain the variation in species richness and plant cover. According to the mean rank of loadings (Table 7), the length of the growing season and the altitude were the most important re-

TABLE 6. Pearson product-moment correlation matrix of environmental variables for four free-flowing and four regulated rivers in northern Sweden. Local factors refer to the river margin.

Variable	Local factors								
	Regional factors				Width of river	Regulated flow			
	Growing season	Latitude	Catchment area	Altitude		All sites	Reservoirs only	New river margin	
Regional factors									
Growing season	1.00								
Latitude	n.s.	1.00							
Catchment area	0.76	n.s.	1.00						
Altitude	-0.86	n.s.	-0.83	1.00					
Local factors									
Width of river	n.s.	n.s.	n.s.	n.s.	1.00				
Regulated flow, all sites	n.s.	-0.42	n.s.	n.s.	n.s.	1.00			
Regulated flow, reservoirs	n.s.	n.s.	n.s.	n.s.	n.s.	0.82	1.00		
Regulated flow, new river margin	n.s.	n.s.	n.s.	n.s.	n.s.	0.67	0.72	1.00	
Height	n.s.	n.s.	n.s.	n.s.	0.44	n.s.	n.s.	n.s.	
Width	n.s.	n.s.	n.s.	n.s.	0.43	n.s.	n.s.	n.s.	
Peat	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	
Clay + silt	0.38	n.s.	n.s.	-0.44	n.s.	n.s.	n.s.	n.s.	
Sand + gravel	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	
Stones	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	
Bedrock	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	

Note: Significant correlations after sequential (Holm 1979) Bonferroni correction (the Dunn-Šidák method [Sokal and Rohlf 1995]) are shown; n.s. = nonsignificant.



TABLE 7. Partial least-squares (PLS) regression of species richness (species-density values) and plant cover in relation to environmental characteristics for four free-flowing and four regulated rivers in northern Sweden. Local factors refer to the river margin.

Dependent variable	Regional factors				Local factors			
	Growing season	Latitude	Catchment area	Altitude	Width of river	Regulated flow		
						All sites	Reservoirs only	New river margin
<b>SPECIES RICHNESS</b>								
Total	0.30	-0.13	0.27	-0.32	-0.27	-0.33	<b>-0.37</b>	<b>-0.41</b>
<b>Morphology</b>								
Trees + shrubs	<b>0.47</b>	-0.28	<b>0.38</b>	<b>-0.44</b>	-0.25	-0.08	-0.13	-0.18
Dwarf shrubs	<b>-0.50</b>	0.37	<b>-0.43</b>	<b>0.43</b>	0.13	-0.20	-0.15	-0.11
Graminoids	0.22	-0.09	0.18	-0.23	-0.30	<b>-0.35</b>	<b>-0.40</b>	<b>-0.45</b>
Forbs + ferns	0.30	-0.13	0.28	-0.32	-0.28	-0.33	<b>-0.39</b>	<b>-0.43</b>
<b>Life cycle</b>								
Annuals + biennials	<b>0.45</b>	-0.21	<b>0.44</b>	<b>-0.47</b>	-0.21	-0.17	-0.19	-0.22
Perennials	0.25	-0.11	0.21	-0.26	-0.29	-0.35	<b>-0.41</b>	<b>-0.45</b>
<b>Naturalness</b>								
Ruderal species	<b>0.49</b>	-0.25	<b>0.47</b>	<b>-0.49</b>	-0.19	-0.08	-0.12	-0.13
Natural species	0.19	-0.08	0.15	-0.20	-0.29	<b>-0.38</b>	<b>-0.43</b>	<b>-0.48</b>
<b>Location</b>								
Aquatic species	<b>0.49</b>	-0.30	<b>0.42</b>	<b>-0.46</b>	-0.23	-0.08	-0.11	-0.17
Riparian + terrestrial spp.	0.18	-0.05	0.16	-0.21	-0.28	<b>-0.39</b>	<b>-0.45</b>	<b>-0.48</b>
<b>PLANT COVER</b>								
Herbs + dwarf shrubs	0.30	-0.10	0.29	-0.33	-0.21	<b>-0.38</b>	<b>-0.40</b>	<b>-0.41</b>
Trees + shrubs	<b>0.36</b>	-0.28	0.26	<b>-0.32</b>	-0.30	-0.25	-0.28	<b>-0.31</b>
Mean rank of loadings	4.9	9.9	7.0	4.5	7.1	7.3	5.7	5.1

Notes: The indicated values are the independent variables loading in the first component. The three highest loadings in each model are boldfaced.

length of growing season and latitude were important predictor variables (Table 7). Furthermore, the coefficients of determination for the regressions were lower in this study ( $R_{adj}^2 = 0.28-0.50$ ; Table 7) than in the previous one ( $R_{adj}^2 = 0.21-0.77$ ; Nilsson et al. 1991a).

#### DISCUSSION

First, we discuss the results of the two comparisons of rivers, then the likely mechanisms causing the differences between free-flowing and regulated rivers, and last the factors controlling river-margin vegetation.

##### *Comparison with the previous study*

The fact that results of the present and previous (Nilsson et al. 1991a) comparisons were largely similar suggests generality, and hence predictability, of the effects of regulation on riparian vegetation along boreal rivers. Although the floristic differences between the free-flowing Pite River and the regulated Skellefte River were not statistically significant, this is more related to the naturally low species richness per site along the Pite River, than to a lack of regulation effects. The Skellefte River had the same low values of local species richness as the other regulated rivers under consideration (Table 2, Nilsson et al. 1991a), suggesting that the magnitude of effect may vary with preregulation conditions, but that regulation leads to convergence in species diversity. However, the coefficients of variation for mean species richness per river were similar be-

tween the free-flowing and the regulated rivers (16% and 13%, respectively)—not supporting convergence.

The present study confirms the results of Nilsson et al. (1991a) in that species richness in the regulated rivers was lower for most species groups, and in no case higher compared to free-flowing rivers. One might ask whether no plant life-history strategy benefits from regulation, because in many terrestrial and aquatic ecosystems disturbance favors species with appropriate adaptations, either to resist the disturbance or to escape it in space or time (White 1979, Gill 1981, Sousa 1984). The answer is probably that many regulated river margins are so different from natural environments that no species are adapted to them. An alternative explanation would be that species with a potential to proliferate on regulated river margins have not yet colonized after regulation. For example, in other parts of the world both native and non-native species have invaded or increased in abundance on river margins following flow regulation (Pautou et al. 1992, Johnson 1994, Busch and Smith 1995, Décamps et al. 1995, Friedman et al. 1997), but exotics are still largely absent from river margins in northern Sweden (Nilsson et al. 1993).

In the previous study (Nilsson et al. 1991a), the number of annual and biennial species per site did not differ between the free-flowing and the regulated rivers, but in this study the free-flowing Torne and Kalix rivers had more such species per site than the regulated Lule River. Organisms with short generation times are often

TABLE 7. Extended.

Local factors							
Height	Width	Peat	Clay + silt	Sand + gravel	Stones	Bedrock	$R_{adj}^2$
-0.23	-0.20	0.00	<b>0.37</b>	-0.07	-0.18	-0.24	0.35
-0.21	-0.25	-0.11	0.29	0.04	-0.22	-0.20	0.35
0.02	0.08	0.23	-0.23	-0.20	0.17	-0.00	0.38
-0.31	-0.22	0.11	0.34	-0.11	-0.20	-0.29	0.32
-0.22	-0.21	-0.01	<b>0.38</b>	-0.06	-0.15	-0.21	0.28
-0.07	-0.08	-0.07	0.36	0.05	-0.26	-0.20	0.34
-0.28	-0.24	0.03	<b>0.35</b>	-0.11	-0.16	-0.25	0.32
-0.03	-0.10	-0.14	0.33	0.09	-0.22	-0.12	0.36
-0.31	-0.25	0.07	0.34	-0.13	-0.14	-0.26	0.30
-0.12	-0.10	-0.06	0.33	0.09	-0.27	-0.23	0.37
-0.29	-0.25	0.05	0.34	-0.14	-0.12	-0.23	0.30
-0.14	-0.11	0.05	0.32	-0.07	-0.24	-0.25	0.50
-0.25	-0.23	-0.01	0.30	-0.04	-0.26	-0.25	0.41
9.5	10.6	13.3	4.0	13.2	9.5	9.3	

favoured in human-made ecosystems, but such species also benefit from natural formation of disturbance patches (Grime 1979, Pickett and White 1985, Huston 1994). In areas with recurrent ice formation, ice scouring may damage or remove plants and create patches of bare soil on lakeshores and river margins, predominantly during the spring flood (Bégin and Payette 1991, Bélanger and Bédard 1994). Ice scouring of riparian zones occurs regularly in the Torne and Kalix rivers during the spring flood (Raab and Zachrisson 1984, Nilsson et al. 1989), but is infrequent in the Vindel River. On the shorelines of storage reservoirs and run-of-river impoundments, lacking spring floods, ice scouring during floods is unimportant, but ice push may be considerable (Sundborg 1977). However, on shorelines along storage reservoirs, annual species often do not have time to complete their life cycles before becoming submerged during reservoir filling in the summer (Nilsson 1981). The difference in ice disturbance between rivers might also explain why tree and shrub species were more species rich in the free-flowing river of the previous study, but did not differ in richness between groups of rivers in this study (Table 3). In the northernmost rivers, recurrent ice disturbance limits the development of woody plants, producing tree-less river margins in the most ice-disturbed parts of the rivers (Julin 1963, Arnqvist and Dynesius 1987).

#### *Type of regulation*

The results of the comparisons between types of water-level regime suggest that river-margin vegetation

responds differently to different types of regulation (Table 4). Regulated but unimpounded reaches were most similar to free-flowing rivers, with nearly identical species-richness values as those of free-flowing rivers. In contrast, storage reservoirs and run-of-river impoundments were most dissimilar in species richness to the free-flowing rivers, whereas the status of the reaches with reduced discharge is uncertain due to the low statistical power of the comparisons.

The hydrology has been modified in fundamentally different ways in storage reservoirs (changed timing and increased intensity of water-level fluctuations) and run-of-river impoundments (increased frequency of water-level fluctuations) compared to free-flowing rivers. Despite that, these changes had similar effects on the shoreline vegetation, because both storage reservoirs and run-of-river impoundments had lower number of plant species per site and sparser plant cover, compared to the free-flowing rivers. This suggests that river-margin plants are sensitive both to increased frequency and changed timing of water-level fluctuations. River margins comprise a gradient from rarely to frequently flooded habitats perpendicular to the channel. Wetland and riparian plant species respond even to small changes in water levels between years (e.g., Ekzertzev 1979, Nilsson 1981, van der Valk 1981, Keddy and Reznicek 1986). Thus, all changes in the flow regime are likely to modify plant zonation, e.g., by contracting part of the land-water gradient. The result could be large changes in vegetation without changing species richness. Indeed, in both storage reservoirs and



run-of-river impoundments the middle and lower parts of the shorelines are flooded during most of the growing season, and the habitat availability for riparian and terrestrial plants thus reduced (Nilsson and Keddy 1988). However, the observed differences in species richness between types of flow regimes suggest that the effects of flow regulation go beyond adjustments in plant zonation.

All the four major types of regulation had more coarse-grained river-margin soils compared to free-flowing rivers. Nilsson et al. (1991a) found a similar difference in their study and explained it as an effect of flow regulation. Regulated water flows increase the erosion of the river margins, and deposit finer materials below the drawdown level and not on the floodplain (Petts 1984). Reservoirs and impoundments act as sediment traps, and when clear water is released from dams, it causes erosion because of its large potential to increase its load of suspended material (Galay 1983, Williams and Wolman 1984, Church 1995). The erosion could reduce plant cover and species richness either because colonizing plants are killed, or because there is less habitat for plant growth in coarse-grained soils. However, there are sites along free-flowing rivers, e.g., along rapids, that have high species richness despite coarse substrates (R. Jansson, C. Nilsson, M. Dynesius, and E. Andersson, *personal observations*). This leaves differences in hydrology as the most probable explanation, acting either directly by drowning or desiccating plants, or by making soils unstable due to erosion.

#### *Dispersal traits*

The finding that species with good dispersal capacity (i.e., wind-dispersed and long-floating species) were the best survivors/recolonizers on shorelines along storage reservoirs, run-of-river impoundments, and reaches with reduced discharge may depend on their ability to reinvade after frequent local extinctions caused by artificial water-level fluctuations (cf. Fahrig 1991). This is not expected on margins along regulated but unimpounded reaches, where water-level fluctuations often maintain natural rhythm and flow peaks are often decreased. A similar case for the importance of colonization was described by Malanson and Kay (1980) and Malanson (1982), who found that river-margin cliffs had rapidly colonizing ferns and mosses on the most frequently flood-disturbed sites, and slower colonizers, including herbs and trees, on more rarely flooded sites. Alternatively, the poor dispersers could potentially survive on regulated river margins, but have failed to recolonize after becoming extinct at the onset of regulation, due to dispersal barriers. If so, river margins created at the onset of regulation should have the least poor dispersers. Indeed, margins along run-of-river impoundments created by raising water levels, which left the former river margin permanently flooded, had lower proportions of species with no special device for dispersal than did river margins on pre-

riparian soils (40 vs. 46%,  $n = 18$  and 6 river-margin sites, respectively,  $P = 0.021$ ,  $t$  test, two-tailed probability). However, river margins on preupland soils may also be more disturbed because they are prone to strong erosion for several decades after regulation (Sundborg 1977).

The fact that the proportion of "long floaters" increased in run-of-river impoundments seems to contradict the notion that hydrochores are unlikely to spread between reservoirs. However, diaspores can still float around within reservoirs, and may do so for considerable periods of time in the absence of currents until washed ashore. "Short floaters" will not be favored in their dispersal by situations that require long floating times, and their chances to reach and invade reservoir shorelines will be smaller compared to the long floaters. Thus, the relative increase in long floaters may be explained by better colonization abilities compared to short floaters. Alternatively, it could be that short floating times are correlated with other traits that are disfavored in regulated rivers. Note that an increase in the proportion of long floaters should be offset by a decrease in short-floaters, because all species are either long or short floaters, but all species could not be classified.

The negative effects of regulation on the local river-margin habitat may thus be amplified by restrictions of dispersal pathways. Such modifications are entailed both by the fragmentation of the river corridor by dams, increasing the distance between source populations and colonizable patches, and by the unnatural water-level regimes with low flow velocities and low capacities for dispersing organisms and litter (Nilsson et al. 1993). For example, spring floods that may carry large quantities of diaspores along with litter in northern free-flowing rivers, are absent or rare (Nilsson and Grelsson 1990). In the free-flowing rivers, short floaters may be dispersed by the high-velocity spring floods, floating or adhered to floating objects such as packs of organic litter (Nilsson et al. 1993). The high current velocity of free-flowing rivers results in a large capacity to carry objects heavier than water, and diaspores may be transported long distances in a short time, making good floating ability less important. Furthermore, establishment varies along gradients of elevation (Jones et al. 1994), substrate texture (Keddy and Constabel 1986), litter deposition (van der Valk 1986), wave disturbance (Wilson et al. 1985), and timing of floods (Johnson 1994). Thus, there is good reason to expect that species with different dispersal strategies may respond differently to river regulation.

#### *Relationships between vegetation and environment*

The importance in the regression models of both regional factors, such as length of the growing season, and local factors, such as water-level regime, suggests that river-margin vegetation is governed by factors working on many spatial and temporal scales (Shmida

and Wilson 1985, Auerbach and Shmida 1987, Reed et al. 1993). Regional factors set the size of the pool of species that potentially can survive locally. However, species are often absent from suitable, local patches because no propagules have arrived there (Primack and Miao 1992a, Tilman 1997).

The monotonic increase in the number of species downstream along the rivers contradicts previous findings that plant species richness peaks in the middle reaches of free-flowing rivers (Nilsson et al. 1989, Décamps and Tabacchi 1994), but is explained by the fact that only linear models were tested for. Some groups of species, such as dwarf shrubs, increased in species richness upstream. Most dwarf shrubs are evergreen, a trait promoted in unproductive environments where acquisition of mineral nutrients is limited (Chapin 1980, Chabot and Hicks 1982, Aerts 1995). Most dwarf shrubs (in this case species of the family Ericaceae) also have ericoid mycorrhiza, which is effective in acquiring nutrients in the nutrient-poor soils with accumulating, slowly decomposing humus layers characteristic of high altitudes and latitudes (Read 1991). This may explain why dwarf shrubs increased in richness towards higher altitudes.

Two other examples show that the relationship between regional factors and vegetation may have different mechanistic explanations for different functional groups. The number of ruderal species per site increased with growing season and catchment area, but this is most likely because ruderal species are associated with agricultural activity, and cultivation in the river valley increases towards the coast (Nilsson and Jansson 1995). The increase in the number of aquatic species towards the coast probably relates to the increasing length of the growing season and to the decreasing duration and thickness of ice cover (Lohammar 1965). The water level of free-flowing rivers and lakes in northern Sweden decreases gradually during winter, and the lower parts of the river margins are covered by ~1-m-thick ice that is lifted by the spring flood, pulling away vegetation frozen into the ice. Only a few species can withstand these conditions, e.g., isoetids such as *Subularia aquatica*, *Ranunculus reptans*, and *Eleocharis acicularis* (Renman 1989). Many aquatic species can still be regionally present in areas with long duration of ice cover but are confined to greater water depths without bottom freezing (Lohammar 1965), and thus do not occur on river margins or lake-shores according to our definition.

#### *Toward a general model*

The ultimate responses of river-margin plant communities to river regulation depend on three factors: (1) the preregulation environmental conditions, such as variation in biogeography, climate, and soil; (2) the operations during the construction of dams, power stations, etc.; and (3) the environmental conditions during the following successional trajectory.

The likelihood that ecological effects of similar structures and operations of regulation vary with location is little explored (but see Friedman et al. [1997]), because regulation measures usually vary between regions. The response to a similar type of development may also vary longitudinally along rivers (Ward and Stanford 1983). Nilsson and Jansson (1995) found that plant species richness was most reduced in the middle reaches of regulated rivers, and this result could not be explained by the type of regulation.

Although modifications of natural flow regimes lead to changes in riparian vegetation, there is no consensus among studies on the direction of these changes (Naiman and Décamps 1997). In many temperate regions, reductions in the depths and durations of flow peaks have caused riparian pioneer communities to be replaced by later successional stages, often dominated by trees (Bren 1992, Johnson 1994, Scott et al. 1997). Most of these changes have occurred in reaches downstream of dams. In northern Sweden such reaches are rare, and species richness and plant cover are lowest along reservoir shorelines, where flood duration has increased following regulation. Flow reductions are often accompanied by reductions of the riparian water table at higher elevations, with losses of deciduous trees due to drought stress (Rood and Mahoney 1990, Rood et al. 1995). Such effects are most pronounced in arid regions (Stromberg and Patten 1990). Reductions in the load of suspended material downstream of dams often lead to erosion and channel incision (Williams and Wolman 1984, Bradley and Smith 1986, Johnson 1994, Friedman et al. 1997). Changes in channel geometry are comparatively unimportant in regulated rivers in northern Sweden, because most river reaches are impounded, and particle sizes are often too large to be moved by the stream.

Boreal rivers differ from temperate ones in that ice disturbance may be important during winters and spring floods (Nilsson et al. 1993). Regulated flows may increase the role of ice action in disturbing river margins. During winter drawdowns, ice subsides onto the shoreline that freezes, killing off plant colonists (Nilsson 1981). Frequent changes in water levels, as in the run-of-river impoundments, cause ice breakage along the shorelines, with moving and displacement of riparian soils.

One of the most important factors at the onset of regulation is whether the regulated river margin is located within, above, or below the preregulation riparian zone (Nilsson et al. 1997). The reason why situations where new margins develop in former uplands are the most negative to plant species richness is probably because postregulation succession starts with few species at hand, and with intense erosion of the river-margin soil (Sundborg 1977). Although species richness did not vary with the time since regulation for any of the types of regulation, we cannot conclude that time is unimportant because most hydroelectric schemes in the

TABLE 8. Suggested relative differences between boreal river margins along free-flowing rivers and along reaches with four major types of regulated water-level regimes.

Variable	Free-flowing rivers	Storage reservoirs	Run-of-river impoundments	Reaches with reduced discharge	Regulated but unimpounded reaches
Local habitat factors					
Heterogeneity	high	low	low	moderate	moderate
Complexity	high	low	low	moderate	moderate
Availability	high	low	moderate	moderate	moderate
Disturbance intensity	moderate-high	very high	low	low (occasionally high)	low-moderate
Disturbance frequency	low	low	high	low	low
Regional, between-site factors					
Corridor function	good	bad	bad	bad	moderate-good
Dominant colonization vector	various	wind	water	wind	various
Source of immigration	upstream + surrounding populations	surrounding populations	surrounding populations	surrounding populations	upstream + surrounding populations
Area of available species pool	large	moderate	small	moderate	moderate-large

study were of similar ages, or between 20 and 40 yr old. In a chronosequence of regulated sites, Nilsson et al. (1997) found that there were few species and sparse vegetation cover on the margins soon after the onset of regulation. In the following decades, many species colonized, but species richness remained impoverished compared to free-flowing rivers.

Table 8 summarizes the most important factors for river-margin plant species diversity during postregulation succession, and how these factors are hypothesized to differ between free-flowing rivers and rivers with any of four major types of regulation, on local as well as regional scales.

Local habitat conditions have been modified differently depending on the type of flow regulation. Natural river margins have high habitat heterogeneity because natural river flows scour some margins and deposit sediment on others (Hupp and Osterkamp 1985, Kalliola and Puhakka 1988) and because flow velocity varies along free-flowing rivers (Nilsson 1987). The riparian zone has high complexity, with zonation of plants along the flood-duration gradient. River margins along regulated reaches that are unimpounded or have reduced discharge may still be fairly heterogeneous and complex, with zonation of plants, as long as semi-natural floods and variation in flow velocity remains. In contrast, reservoir shorelines are spatially homogeneous, and habitat complexity is reduced, as plant zonation is lost. The lower habitat heterogeneity is supposed to reduce the differences in plant species composition among river-margin sites (i.e., lower  $\beta$ -diversity) subject to similar types of water-level regime.

For most plant species, habitat availability is reduced on regulated river margins (Table 8), as shown by lower percentage plant covers for all types of regulation. This is probably because fine-grained soils are eroded, and (on reservoir shorelines) flood duration is increased. Habitat disturbance on margins along storage reservoirs and run-of-river impoundments is increased because of changed intensity or frequency of water-level

fluctuations, and these effects are strengthened by ice. In contrast, river margins along regulated reaches that are unimpounded or have reduced discharge may be less disturbed in the absence of floods. However, margins along reaches with reduced discharge may occasionally be strongly disturbed during flow peaks. The relative importance of local habitat factors in explaining the low plant species richness in regulated rivers is not clear, because knowledge of how natural fluctuations in flow and water level affect lakeshore and riverbank vegetation (e.g. van der Valk 1981, Keddy 1983, Nilsson 1987, Day et al. 1988, Hughes 1990) may not be applicable outside the range of natural flows (but see Stevens et al. [1995]). The floristic response to changes in water-level regime also depends on how sediment and litter dynamics (Hupp and Osterkamp 1985, Salo et al. 1986, Nilsson and Grelsson 1990, Kalliola et al. 1991), plant establishment (Fenner et al. 1985, Rood and Mahoney 1990, Hughes 1994), and riparian water tables (Rood et al. 1995) are affected. Studies are needed in which the effects of these processes are separated. For example, one might ask whether adding fine-grained soils to eroded river margins could mitigate the negative effects of regulated water levels. Another question would be about the relative effects of regulated water levels and changes in river-margin water tables. As a matter of fact, soils with periodically effluent groundwater are common in riparian zones and favor high plant species diversity (R. Jansson, C. Nilsson, M. Dynesius, and E. Andersson, *personal observations*). When water levels are raised by damming, new river margins are created in terrace or hill-slope soils where effluent groundwater is usually less frequent.

River regulation also affects regional, between-site factors (Table 8). Dams cause fragmentation of the riparian corridor and are barriers to long-distance hydrochory, thus reducing the corridor function. However, corridor function may still be good along unimpounded reaches downstream of dams if natural flow

patterns are retained. Modifications of the water-level regime may change the importance of different colonization vectors and recruitment patterns. For example, reductions in flood peaks may hamper recruitment of some riparian species, as in the case with cottonwoods (*Populus* spp.) along streams in western North America (Fenner et al. 1985, Rood and Mahoney 1990). In the present study, the proportion of anemochores increased in the shoreline floras of storage reservoirs and reaches with reduced discharge, while the proportions of species without any special device for dispersal decreased. This suggests that the ability to recolonize following local extinction may be critical. In run-of-river impoundments, hydrochory may be effective, but primarily for long-floating species, which will be stranded on the river margin, while short floaters may sink.

Since dams block populations from dispersing downstream by water, surrounding populations should be the main source of immigration to regulated river margins, and the similarity in species composition between river margins and nearby uplands likely increased. The break-up of the river continuum suggests that differences in species composition between impoundments may be considerable. However, on river margins along unimpounded reaches, downstream dispersal may be effective, but the distance to the nearest upstream dam determines the area of the available species pool (Zobel 1997). Where dispersal ability is likely to be important for local persistence, as in storage reservoirs and reaches with reduced discharge, the area of available species pool may still be fairly large, but constrained to species with good dispersal ability.

#### *Study implications*

Plant species richness and cover were reduced in run-of-river impoundments and in storage reservoirs, which both experience water-level fluctuations that are rather different from the natural situation. However, the smallest deviation from free-flowing water-level regimes able to produce such reductions is unknown. To maintain different structures of river-margin vegetation we need to know what durations and frequencies of flooding they require (Richter et al. 1997). Up to now, hydroelectric schemes have not been designed to minimize losses of ecological integrity. In the future, river managers will face increased demands to make river flows available also for uses other than power production, such as conservation of biodiversity, drinking water supply, irrigation, and recreation (Postel et al. 1996). Presently, we do not know the relationships between deviations from natural flows and losses of ecological integrity. The relationship may be more or less linear, or there may be certain thresholds. If thresholds are present, as described by Scott et al. (1997), it is important to identify them, and to let regulated flow regimes match those thresholds in order to reduce perturbations to the biota. Experimental flooding may be extremely helpful in identifying the size and frequency

of necessary floods (Barinaga 1996, Wuethrich 1996, Collier et al. 1997). Dam removals (Schuman 1995) and reregulation of flows (Hesse 1995, Petts 1996) are complementary strategies to test how much of the river's ecological integrity can be rehabilitated.

The relationship between the dispersal capacities of species and their responses to regulation highlights the need to consider large-scale spatial processes when evaluating the effects of human exploitation. The outcome is not only determined by the ability of biota to survive in the local environment; the ability to get there is equally important. For example, species with good dispersal capacities were the best survivors on reservoir shorelines as well as on margins along reaches with reduced discharge. This emphasizes the need for studying both the corridor functions of rivers and the relative importance of surrounding biota in supplying rivers with new organisms. Studies separating the effects of river-corridor fragmentation per se from local site disturbances are called for. Comparisons of the effects of river regulation between biogeographic regions are also likely to contribute substantially to our knowledge about riparian plant ecology.

#### ACKNOWLEDGMENTS

We thank Francine Hughes, Rebecca Sharitz and anonymous reviewers who improved the manuscript with their comments. Björn Carlberg, Alf Ekblad, Maria Gardfjell, Gunnel Grelsson, Mats E. Johansson, and Ulf Sperens assisted in the 1985–1988 fieldwork. Lena Kjällgren assisted in the processing of primary data, and Tom Korsman helped with the PLS regressions. This work was funded by the Swedish Natural Science Research Council and the Swedish Society for the Conservation of Nature (grants to C. Nilsson).

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