

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/234058106>

Aquatic plant diversity in riverine wetlands: The role of connectivity

Article in *Freshwater Biology* · March 1998

DOI: 10.1046/j.1365-2427.1998.00273.x

CITATIONS

203

READS

345

3 authors, including:



Gudrun Bornette

French National Centre for Scientific Resea...

99 PUBLICATIONS 3,666 CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:



relationships between wetland functioning and pathogens. [View project](#)

Aquatic plant diversity in riverine wetlands: the role of connectivity

GUDRUN BORNETTE,* CLAUDE AMOROS* AND NICOLAS LAMOUREUX†

*Laboratoire de dynamique des écosystèmes aquatiques péri-fluviaux et génie écologique; E.S.A. C.N.R.S. 5023, Ecologie des Eaux Douces et des Grands Fleuves, Université Claude Bernard Lyon I, 69622 Villeurbanne Cedex, France

†Compagnie Nationale du Rhône & E.S.A. C.N.R.S. 5023, Ecologie des Eaux Douces et des Grands Fleuves, Université Claude Bernard Lyon I, 69622 Villeurbanne Cedex, France

SUMMARY

1. The hypothesis was tested that intermediate connectivity to a river results in propagule inputs to wetlands, whereas excessive connectivity impedes recruitment, and insufficient connectivity causes less competitive species to be eliminated, with no recruitment of new species. As a consequence, very low or very high nutrient levels should decrease species richness by selecting specialized species, whereas intermediate nutrient levels should favour the co-occurrence of species with contrasting nutrient requirements.
2. Among cut-off channels with high sinuosity and which are infrequently flooded by the river (low flood scouring), one example possesses high species richness because most species are saved from extinction by long-term isolation of the channel and cold groundwater supplies. Other channels are poorly supplied with groundwater and show a lower richness of species, because of low propagule inputs and low recruitment potential.
3. Cut-off channels with low sinuosity and which are flooded at intermediate frequencies were divided into three groups. The first group was species-poor, being closely connected to the river through downstream backflows which maintain nutrient-rich and turbid waters, in keeping with the hypothesis. The second group presents intermediate richness caused by: (i) lower river backflows; and (ii) floods that partly scour substrate and plants, and afford regeneration niches for transported propagules. The third group was species-poor because of excessive groundwater supplies, which probably acted as a limiting factor for species growth and recruitment.
4. The most frequently flooded channel shows the highest species richness, and occurrence of rare and fugitive species, because of floods which compensate competition by scouring sediments and plants, and afford regeneration niches for propagules. In this case, conservation of biodiversity necessitates propagule sources at the level of the river landscape.

Introduction

Large river cut-off channels are currently considered as a high source of productivity and diversity in fluvial hydrosystems (Drago, 1976; Holcik *et al.*, 1981). This diversity results from: (i) ecological succession occurring in these slow-flowing or stagnant water-bodies (in contrast to the main river channel); and (ii) episodic connections with the river during floods, which carry

and import animals, plants and suspended material (Schneider & Sharitz, 1988; Nilsson, Gardfejjell & Grelsson, 1991a). Succession can be partially re-set by these flood disturbances, permitting the co-occurrence of communities from diverse successional stages (Bravard, Amoros & Pautou, 1986; Foeckler, Diepolder & Deichner, 1991). Connell (1978) formulated the

'intermediate disturbance hypothesis'; that is, that disturbances with intermediate frequency and magnitude permit the co-occurrence of fast-growing and competitive ruderal species, promoting a great richness and diversity of species. Such a pattern has been observed in wetlands (Keddy, 1983; Nilsson *et al.*, 1991b), where intermediate frequency of disturbances, depending in some cases on connectivity between the wetland and the river, favours the maintenance of rare species that are usually weakly competitive (Wisheu & Keddy, 1991; Bornette & Large, 1995).

Cut-off channels are progressively disconnected from the river, first upstream and then downstream, by alluvial deposition resulting from geomorphological processes and ecological successions (Petts & Amoros, 1996). Surficial connections between wetlands and the river remain as long as the downstream end of the cut-off channel remains open to the river; in this case, the influence of the river on the wetland depends on the ability of backflows to go farther into the cut-off channel (Juget *et al.*, 1979). Wetlands that are closed at both ends may only be connected during floods, when the river overflows through their upstream end. In this case, the frequency of surficial connections between the river and the wetland depends on the river's overflowing frequency. Amoros & Roux (1988) and Amoros (1991) assume that connectivity between cut-off channels and the river involves all fluxes of water, material and living organisms between these two compartments. Depending on the various forms of connections quoted above, the degree of connectivity between cut-off channels and the river varies from very low (infrequent connections) to very high (permanent connections).

Other connections that involve slow or no fluxes of material and living organisms also occur between cut-off channels and groundwater aquifers (seepage from the river or inputs from any hillslope aquifer). Such connections are reduced or even prevented when, during succession, production and deposition of organic matter progressively clog the bed of the cut-off channel (Rostan, Amoros & Juget, 1987). This disconnection does not occur if sufficient groundwater fluxes sustain fine sediment removal from the channel bed (Bornette, Amoros & Chessel, 1994a). River seepage is usually richer in nutrients than hillslope aquifers (Bornette & Amoros, 1991; Trémolières *et al.*, 1991). Connections between former channels and hillslope aquifers usually instigate drainage of the hillslope

aquifer via the former channels, and oligotrophication of the wetland if this aquifer is effectively nutrient-poor (Bravard *et al.*, 1997).

A combination of these processes results in a high diversity of habitat conditions in these cut-off channels at the fluvial landscape level (Cellot *et al.*, 1994). This diversity is reflected by the divergent results obtained by authors who compare species richness in riverine wetlands with that of a main river channel. Lloyd & Walker (1986) demonstrated that fish species richness is high in the main channel, intermediate in backwaters still connected at their downstream end, and low in backwaters surficially disconnected from the river, but they did not indicate the degree of temporary connectivity of these backwaters with the river (particularly due to floods). Conversely, Roberts & Ludwig (1991) observed a greater richness of species in backwaters and channels disconnected from the main channel at both ends, and they attributed this observation to water-level fluctuations that increase recruitment in these wetlands. Because connectivity continuously decreases due to natural processes and human impact (Amoros, 1991), the issue of preserving or restoring connectivity is of primary importance in the environmental management of large rivers (Ward & Stanford, 1995).

The present paper aims to delineate the effects of connectivity, between cut-off channels and a river, on aquatic plant diversity or rarity, in order to provide recommendations for their conservation. The hypothesis was that intermediate connectivity allows propagule inputs into the wetlands, without impeding their recruitment, which promotes high species richness. Conversely, high connectivity impedes recruitment either by over-frequent flood scouring or by supplying nutrient-rich and turbid surficial waters to the wetland, which reduces species richness. In the same way, too low a connectivity should decrease flood scouring and succession rejuvenation, and thus allow competition to eliminate the less competitive species, with no recruitment of new species by propagule import during floods. As a result, species richness and the number of rare species should decrease. The effect of connectivity with groundwater should depend on its origin; thus an ecosystem supplied by both groundwater from nutrient-poor hillslope aquifers and nutrient-rich river seepage should present intermediate nutrient levels, favouring greater species richness, on account of the co-occurrence of species

possessing contrasted nutrient requirements. Very low or very high nutrient levels should decrease species richness by selecting specialized species.

To test these hypotheses, links between surficial connectivity, connectivity with groundwater and two expressions of community diversity are considered. Community diversity is assessed through species richness and through the relative rarity of species occurring in cut-off channels.

Materials and methods

Study sites

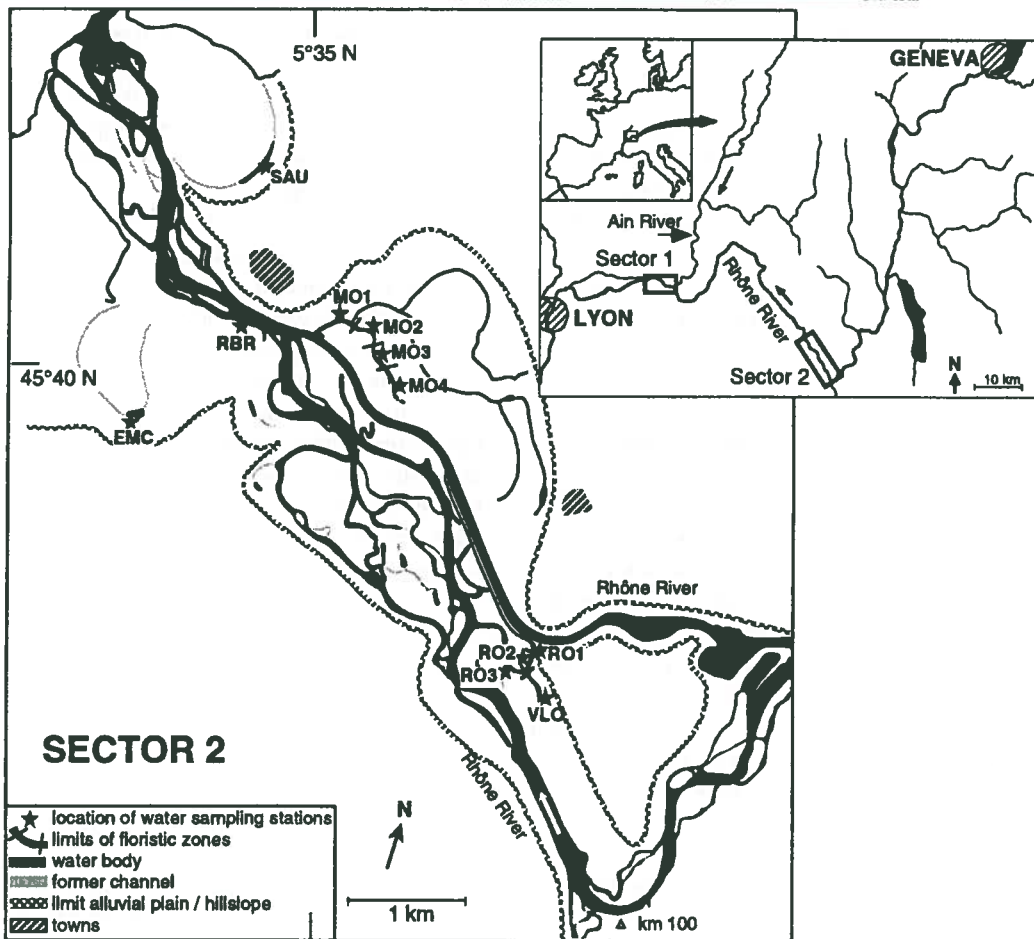
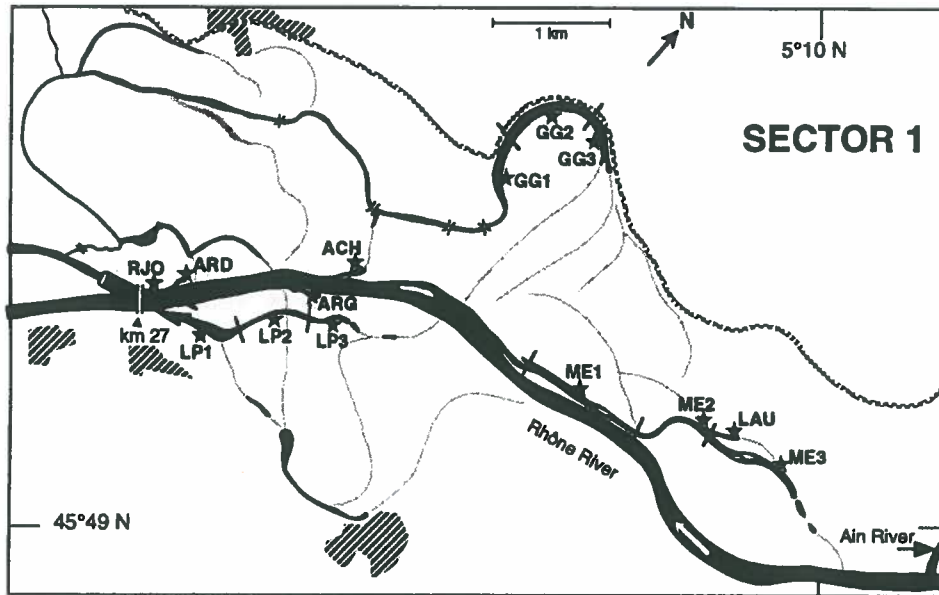
The study was carried out on twelve cut-off channels of the Rhône River (France). All are disconnected from the river upstream at mean water level, and two are disconnected at both ends. Four channels are indirectly connected to the river through a secondary channel, itself connected to the river (LAU, MOR, VLO, ROS, Fig. 1). Channels present various overflowing frequencies (as they are inundated by the river from 0 to 37 days yr⁻¹; Table 1) and aquatic plant communities (Table 2), ranging from oligotrophic communities with *Potamogeton coloratus* to eutrophic communities with *Ceratophyllum demersum* and *Lemna minor* through to mesotrophic communities with *Groenlandia densa*, *Callitriche platycarpa* and *Berula erecta* (Kohler, Brinkmeier & Vollrath, 1974; Carbiener *et al.*, 1990).

Vegetation

Floristic zonation and species richness. To assess species richness, it was necessary to assess overall spatial heterogeneity that occurred in each wetland. Sampling plots of 2-m-wide strips crossing the channels and evenly distributed along the upstream–downstream gradient made it possible to consider both: (i) longitudinal heterogeneity occurring along channels; and (ii) transverse heterogeneity from the deepest part of the channel to the banks. Aquatic vegetation was surveyed during the summer of 1993 using the double Braun-Blanquet (1932) cover and sociability scales. The cover index recorded species abundance, while sociability focused on patchiness (as opposed to even distribution of species) within the sampling plots. The number of replicate strips of each floristic zone is shown in Table 1. The mean abundance of each species per floristic zone is shown in Table 2.

Species richness was obtained by counting the number of species in the whole sampling set for each cut-off channel. If floristic discontinuities occurred along the channel, floristic zonation was carried out, and species richness was then assessed for each floristic zone. Floristic zonation permits consideration of changes in habitat conditions within cut-off channels that could influence plant recruitment (depth, turbidity, water quality); for example, these zones are supposed to be less influenced by river backflows when they are located far from the downstream confluence. Floristic zones have been demonstrated to be a relevant spatial scale for the study of cut-off channels (Bornette *et al.*, 1994b) and are a way to avoid any methodological bias that could result from differences in wetland length, since longer wetlands could have upstream–downstream gradients in habitat conditions, thereby increasing species richness. Each abundance and sociability data couplet was converted to a single value to facilitate statistical analysis (for conversion rules, see Bornette & Amoros, 1991), and floristic data collected along each channel were analysed using a centred principal component analysis (cPCA; Goodall, 1954). All data sets were analysed using ADE software (Thioulouse *et al.*, 1995). As this analysis provides ordination of the sampling plots on the basis of their floristic composition, floristic zones were delineated within each cut-off channel according to the factorial co-ordinates of the sampling plots along the first two axes of the cPCA. Each floristic zone numbered one corresponded to the downstream end of the cut-off channel. Some channels were not divided into floristic zones by analysis (ACH, ARD, ARG, VLO, LAU, EMC, SAU; cf. Table 1). Species richness was calculated for each channel, and for each floristic zone within channels that included several floristic zones. Species richness per channel did not result simply from the addition of the species richness of the zones, as a given species can occur in several zones within the same channel. Floristic zonation was used in a second step as a sampling frame.

Species richness and community uniqueness. As the number of species does not provide information on the rarity of the species, and as the occurrence of rare species can be favoured by connections between wetland and the river, the relative uniqueness of species content was estimated for each channel. Frequency of occurrence of each species within the twelve



channels was calculated (the most frequent species occurred in nine channels). In a second step, the number of species occurring in each channel, and simultaneously in one, two, three and up to nine channels of the data set was counted. Finally, the percentage of species showing a relative rarity of one, two, three, and up to nine occurrences was calculated for each channel, and represented by a graph. The highest are the values on the left side of the graphs, the most unique are the communities of the channel compared to the whole set of channels.

Connectivity assessment

Surficial connectivity. The degree of connectivity between cut-off channels and the river was assessed through the quantification of: (i) river overflows into the cut-off channels; and (ii) river backflows into the cut-off channels through their downstream outlet. The influence of river backflows can be assessed by water physico-chemistry of the channels (Juget *et al.*, 1979; Ortscheit, 1985).

The frequency of overflowing of the river was derived from the knowledge of: (i) the stage-discharge relationships of the river at the upstream end of each cut-off channel; (ii) the discharge frequency distribution of the river; and (iii) the stage at which water flows into the cut-off channel (Table 1; S. Quignard, unpublished data). As the scouring ability of water during floods depends on its velocity, and as it was not possible to measure velocity during flooding, the variables that have an effect on hydraulic behaviour were documented; that is, the drainage capacity of the channel (mean depth and width) and its relative slope through its sinuosity (Bravard & Gilvear, 1993). Reduction of sinuosity increases the slope within the cut-off channel and therefore the flow velocity and the scouring effect of floods. The set of sampled channels included both channels with low sinuosity (usually a braided pattern, nine channels with sinuosity ranged between 1.07 and 2.6) and high sinuosity (usually a meandering pattern of the river, three channels with sinuosity ranged between 7.3 and 12.8).

The number of substrate classes (coarse \approx 2–

250 mm; sand or sandy silt \approx 0.01–2.00 mm; silt and clay \approx < 0.01 mm, mud, peat) occurring within a floristic zone was visually recorded (Table 1), because it affords information on the net effect of floods: within the same alluvial floodplain, substrate grain-size is indicative of the dominant processes operating in a former channel (erosion vs. deposition; Poff & Ward, 1990; Lamberti *et al.*, 1991). In addition, it can provide a number of microhabitats for aquatic macrophytes (Macan, 1977; Barko & Smart, 1986), and increase species richness.

The data set was analysed through a simple, normalized PCA (nPCA; Goodall, 1954).

Groundwater connectivity. Connections between cut-off channels and either river seepage or hillslope aquifer can be assessed through the physico-chemistry of water (Ortscheit, 1985; Bornette & Amoros, 1991; Trémolières *et al.*, 1991).

Hillslope aquifer is characterized by high nitrate content (measured as $[N-NO_3]$ mg L⁻¹, obtained by ion chromatography), high alkalinity ($[HCO_3^-]$, measured by HCl N/10) and high conductivity ($\mu S\ cm^{-1}$, measured *in situ* with a MERCK device) compared to seepage or river water (Bornette & Amoros, 1991; Bornette & Large, 1995). Water temperature (measured *in situ* with a MERCK device), oxygen concentration (measured *in situ* with a MERCK oxymeter) and silica content (obtained by colorimetry and using the molybdc acid method) can also indicate oxygen-poor stenothermic groundwater supplies. Water inputs from the Rhône River are indicated by higher pH values (measured *in situ* with a MERCK pH-meter) and higher sulphate content (measured by ion chromatograph; Juget *et al.*, 1979). Phosphate (obtained by ion chromatography) and ammonium nitrogen contents (measured by colorimetric method using salicylate) indicate the nutrient content of the water and can indicate anthropogenic inputs from farmland drainage and sewage effluents.

Floristic zonation was used as a sampling frame for measuring water physico-chemistry (Fig. 1). Water samples were collected monthly from each floristic zone from May 1995 to August 1996. Two stations in

Fig. 1 Location of studied wetlands in two reaches of the Rhône River floodplain. Locations of floristic zones and chemical sampling stations are indicated along each former channel, as well as coded labels of zones used in other figures and text. RBR and RJO indicate river sampling stations.

Table 1 Characteristics of the channels under study. For channel location, see Fig. 1. The river floods more frequently (ME1) than the two upstream zones because of a break in the downstream alluvial levee. The channel codes and the floristic zone codes are those used in the following figures. Overflow frequency is expressed as the mean duration of inundation of the channel by river water. For the significance of grain-size classes, see text

Channel	Channel code	Floristic zone codes	Number of sampling plots	Overflow frequency (days yr ⁻¹)	Sinuosity	Mean depth (m)	Mean width (m)	Number of grain-size classes	Species richness per channel		Species richness per floristic zone Total
									Total	Hydrophytes	
Anse de la Chavanne	ACH	ACH	6	9	1.12	0.5	14	3	14	8	14
	ARD	ARD	6	6	1.15	0.85	16	3	12	8	12
	ARG	ARG	4	3	1.04	0.6	22	2	10	8	10
Anse Rive Gauche	EMC	EMC	5	0.01	7.35	0.7	50	1	11	8	11
	GGR	GG1	7	0.01	12.13	0.6	65	1	30	12	14
Grand Gravier	GG2	GG2	12			1.5	100	1			19
	GG3	GG3	8			1.9	65	2			21
	LAU	LAU	5	3.5	1.08	0.5	6	3	11	8	11
Bras à Laurons	LPE	LP1	15	2	1.14	2.4	75	2	18	12	9
		LP2	8			2.1	20	3			6
		LP3	10			1.2	14	3			14
Méant	MEA	ME1	10	37	1.07	2	25	3	38	18	26
		ME2	34	21		0.8	14	3			21
		ME3	20			0.4	10	3			31
Mortier	MOR	MO1	19	3.5	1.33	1.1	15	2	26	17	16
		MO2	10			0.8	15	1			14
		MO3	9			0.5	15	1			19
Sauget	SAU	MO4	10			0.4	14	1			19
	ROS	SAU	8	2	12.86	2	50	1	24	8	24
		RO1	9	3.5	1.46	1.25	14	3	23	13	12
Rossillon	RO2	RO2	3			1.1	15	2			12
		RO3	6			1.1	10	2			18
	VLO	VLO	9	2	1.26	0.25	15	1	21	8	21

the river were also sampled in each floodplain section (RBR and RJO).

Data were analysed through a between-class nPCA. For this analysis, data were normalized then averaged for each sampling station (Table 3). The reduced data of sites against physico-chemical variables were then analysed by simple nPCA, affording an average typology of the sampling stations on the basis of their water physico-chemistry (Dolédec & Chessel, 1991).

Results

Surficial connectivity and species richness

Statistical analysis of data is provided in Fig. 2 (for analysis, the overflow frequency was attributed to each floristic zone within a given channel). The first two axes represented, respectively, 50.7% and 26.9% of inertia of the whole data set.

The F1 axis was positively correlated to the overflow frequency and number of grain-size classes, and negatively correlated to sinuosity and width. The former meandering channels (GG1, GG2, GG3, SAU and EMC), as well as the downstream part of LP1, were plotted in the negative part of the F1 axis, and were characterized by low overflow frequency, high sinuosity, greater width and low substrate heterogeneity. LP1, GG3, SAU and GG2 were also discriminated along the F2 axis, as they presented greater depth, whereas GG1 and EMC have negative scores on the F2 axis and low depth.

Cut-off channels with low sinuosity, intermediate-to-high substrate heterogeneity and overflow frequencies, show positive coordinates along the F1 axis. Axis F2 discriminated low depth channels on the negative part of the axis (VLO, MO4, MO3, MO2 ARG), from the deeper channel (ME1).

Some channels that were rarely connected to the river (GG2, SAU, GG3) and the more frequently flooded channels (ME1, ME2, ME3) both had high species richnesses. Only one significant link was delineated between the F1 coordinates of the stations and species richness (polynomial regression of rank 2; $y = 12.85 + 2.00X + 1.34 X^2$; $P < 0.05$).

Groundwater connectivity and species richness

The first two axes of the between-station nPCA (Fig. 3) represented, respectively, 28.9% and 22.4% of inertia of the whole data set.

Positive scores on axis F1 were related to pH, oxygen content and, to a lesser degree, sulphate content. ARG, ARD, LP1 and, to a lesser extent, LP2 and ACH, were plotted close to the river stations (RJO, RBR) on this part of the factorial map, indicating the high river influence through backflows (although the river never overflowed into the cut-off channels during water sampling). Negative scores on axis F1 were related to high conductivity and silica content, low pH, oxygen and sulphate contents. Stations located on this part of the axis were less influenced by the river water. High conductivity and silica content, and low oxygen content indicate that they are supplied by groundwater. Positive values on axis F2 discriminated stations supplied by hillslope aquifer (MEA, GGR, LAU) with higher nitrate content, conductivity and alkalinity. Hillslope aquifer characterized by high nitrate content was depicted in this area (Reygrobelle *et al.*, 1981). Stations plotted on the negative part of this axis (ROS, VLO) were supplied by river seepage, as indicated by low nitrate and oxygen contents, high ammonia and sulphate contents, together with high conductivity and alkalinity (Bornette & Amoros, 1991). Two channels were plotted in an intermediate position between the two other groups (MOR, SAU), suggesting that they were supplied by both hillslope aquifer and river seepage.

Species richness appeared lower in the stations that were submitted to river backflows (ARG, ARD, LP1, LP2, ACH). The highest values of species richness were observed in most of the stations supplied by river seepage or hillslope aquifer. Only EMC, LAU, RO1 and RO2 had low species richness. Any increase in species richness appeared to be significantly correlated to the decrease in river influence and an increase in groundwater supplies (linear regression: $y = 15.82 - 2.09X$; $P = 0.02$).

Rare species and community uniqueness

The community uniqueness of each channel is indicated in Fig. 4; for example, 8.7%, only two of the twenty-three species occurring in ROS were found only in this channel; 21.7% (five of the twenty-three species) were noted both in ROS and another channel, 17.4% (four of the twenty-three species) occurred in ROS and in two other channels, etc.

Some channels (ARD, ARG, LPE, LAU and EMC) did not present any rare species (i.e. that occur only

Table 2 Average abundance (based on Braun-Blanquet cover-abundance scale) of species in the cut-off channels under study. The abundance of species is given for each floristic zone if several zones occur along the channels. The species that are not strictly aquatic in the studied channels are marked by an asterisk. For the codes of the channels or the floristic zones, see Table 1, and for their location, see Fig. 1

	ACH	ARD	ARG	EMC	GG1	GG2	GG3	LAU	LP1	LP2	LP3	ME1	ME2	ME3	MO1	MO2	MO3	MO4	SAU	RO2	RO3	ROI	VLO
<i>Alisma plantago-aquatica</i> L.*												0.1	0.2					0.222	0.5		0.11	0.333	
<i>Alnus glutinosa</i> (L.) Gaertn.*					0.429							1.3	0.8						0.33	0.7	0		
<i>Alopecurus nequaliz</i> Sobol.*							2.2					2.9	3.38	0.15					0.33	0.33	0		
<i>Berula erecta</i> (Huds.) Coville					0.429							2.6	0.9	0.4	1	0.273	1	1.889	0.25	1	2.3	2.56	0.222
<i>Bidens tripartita</i> L.*		0.166					2.6																1
<i>Callitriche platycarpa</i> Kütz.					0.143									0.4				0.222	0.33				0.444
<i>Callistegia septium</i> (L.) R. Brown.*					0.286	0.83	0.143		0.133										0.5	0.66			1.111
<i>Carex acutiformis</i> Ehrh.*	0.167		1.2	3.857	0.833	0.857		0.67	0.375	1.8								2.875	0.33	0.7			
<i>C. elata</i> All.*												0.5	0.26	0.5	0.2				2.875	0.33	0.7		
<i>C. pseudocyperus</i> L.*																			2.33				
<i>Clara vulgaris</i> L.																							
<i>C. uxor</i> Vaillant						0.167																	
<i>Ceratophyllum demersum</i> L.	2.5	1.666	4.25	7	0.143	4.333	1	2.8	2.75	3.1					0.143	3.91	2.5	0.111	5	0.3			0.778
<i>Cladium mariscus</i> (L.) Pohl*																							
<i>Eleocharis acicularis</i> (L.) Roem. et Schult.*												1.7	0.17	0.1									
<i>E. palustris</i> (L.) Roem. et Schult.*														0.15									
<i>Elodea canadensis</i> Michaux	1.167	2.75					1					0.5	0.64	0.25	0.714	0.636	5.1	1.222	3.5	3.7	3.89	1.889	
<i>Epilobium</i> sp. L.*																					0.3		
<i>Fontinalis antipyretica</i> Hedw.														0.52	0.3								
<i>Frangula alnus</i> Mill.*																			0.125				
<i>Gallium palustre</i> L.*												0.7	1.25						0.875				
<i>Glyceria fluitans</i> (L.) R. Brown												0.1	1.88										
<i>Groenlandia densa</i> (L.) Fourr.												1.5	0.25	0.6							0.33		
<i>Hippuris vulgaris</i> L.					0.286	0.417	0.143	0.4				1.5											
<i>Hottonia palustris</i> L.							0.2					1.8	0.29	0.1		0.182	0.2	0.444					0.222
<i>Humulus lupulus</i> L.*																							
<i>Hydrocharis morsus-ranae</i> L.			1.6																1.25				
<i>Iris pseudacorus</i> L.*			0.25	0.6	0.571							0.2	0.25	0.15					0.111	0.375			0.111
<i>Juncus articulatus</i> L.*																							0.111
<i>J. effusus</i> L.*																							0.22
<i>J. subnodulosus</i> Schrank*																							
<i>Lemna minor</i> L.			0.8																				
<i>L. trisulca</i> L.			0.4																				
<i>Luronium natans</i> (L.) Rafin.							0.571																
<i>Lycopus europaeus</i> L.*																							3.556
<i>Lysimachia nummularia</i> L.*																							2.556
<i>L. vulgaris</i> L.*																							0.111
<i>Lythrum salicaria</i> L.*					0.83	0.429																	
<i>Mentha aquatica</i> L.*					0.143					0.1													0.25
<i>Menyanthes trifoliata</i> L.					0.286							0.1	0.73	0.55									0.375
<i>Menyanthes trifoliata</i> L.					0.83	0.143																	
<i>Myosotis scorpioides</i> L.*		0.833										1.6	0.23	0.4	0.285	0.45	0.1						

Table 2 Continued

	ACH	ARD	ARG	EMC	CG1	CG2	CG3	LAU	LP1	LP2	LP3	ME1	ME2	ME3	MO1	MO2	MO3	MO4	SAU	RO3	RO2	RO1	VLO
<i>Myriophyllum spicatum</i> L.	4.833	1.666	4.5	1.2	0.167	0.429	0.267	0.125	2	0.1	0.14	0.1	0.136	0.4	0.428	0.182	0.3	1	0.875	0.33	1	0.44	0.111
<i>M. verticillatum</i> L.					1.333	2.857	3	0.25	0.6	1.2													
<i>Najas marina</i> L.	1.5	3.833										0.58	0.1						0.33	0.3	0.3	0.11	
<i>Najas marina</i> L.												0.38											
<i>Nasturtium officinale</i> R. Brown *															0.286	0.273	0.6	3.875					
<i>Nitella confertifera</i> (Breb.) A. Br.																							
<i>Nuphar lutea</i> (L.) Smith																							
<i>Nymphaea alba</i> L.																							
<i>Phalaris arundinacea</i> L.*	0.5	0.333	0.75	1.2	3.286	2.75	1.143	0.2	0.3	1.4	0.52	2.25	1.142	0.227	0.9	1.222	1.16	0.7	1.16	0.7	0.778		
<i>Phalaris australis</i> (Cav.) Steud. *	2																						
<i>Polygonum hydropiper</i> L.*	0.667	0.666			5.857	4.5	2.857	0.6	2.267	0.75	1.4	0.1	0.45	1.9	2.333	5.625							2.778
<i>Polygonum hydropiper</i> L.*												0.3	0.45	0.6	1.667	0.33	0.3	0.33					0.333
<i>Potamogeton crispus</i> L.																							
<i>P. coloratus</i> Hornem.					0.83	0.143														0.83	1	1.11	2.667
<i>P. compressus</i> L.																							
<i>P. frutescens</i> L.																							
<i>P. lucens</i> L.					0.25	0.143		0.2	2.9	3.428	3.182	0.2								0.33			0.11
<i>P. uatans</i> L.					0.571	0.333	0.429	0.4				2.7	0.14	0.25									
<i>P. nodosus</i> Poiret			0.5																				
<i>P. pectinatus</i> L.	2.167	1	0.5					0.8	0.1														
<i>P. perfoliatus</i> L.	0.667																						
<i>P. trichoides</i> Cham. et Schlecht.			0.333	0.25																			
<i>P. pusillus</i> L.			0.5	0.5			0.6	0.133	0.2	0.7	0.29	0.4	0.591	1.2	2.667	4	6.7	2.89	1.222				
<i>P. pusillus</i> L.	0.5									3.2			0.143	0.227	0.3	0.111							
<i>Ranunculus circinatus</i> Sibth.					0.286																		
<i>R. lingua</i> L.*																							
<i>R. trichophyllus</i> Chaix			0.166																	0.33			0.22
<i>Riccia fluitans</i> L.															0.136	0.111							
<i>Rorippa amphibia</i> (L.) Besser *																							
<i>Rubus fruticosus</i> L.*	0.333	1.333																					
<i>Rubus fruticosus</i> L.*																							
<i>Sagittaria sagittifolia</i> L.																							0.778
<i>Salix cinerea</i> L.*															1.286								
<i>Scirpus lacustris</i> L.*																							
<i>Scirpus lacustris</i> L.*					0.333	0.571				0.1	0.7	0.29	0.15						0.75				
<i>Scrophularia auriculata</i> L.*					0.143																		
<i>Scutellaria galericulata</i> L.*																							
<i>Senecio aquaticus</i> Hill*																							
<i>Solanum dulcamara</i> L.*																							
<i>Solanum dulcamara</i> L.*																							
<i>Sparangium emersum</i> Rehm.																							
<i>S. erectum</i> L.*																							
<i>Thelypteris palustris</i> Schott*																							
<i>Typha latifolia</i> L.*																							
<i>Typha latifolia</i> L.*					0.167	1.571																	
<i>Urtica dioica</i> L.*					0.143	0.25																	
<i>Urtica dioica</i> L.*																							
<i>Urticularia minor</i> L.																							
<i>U. vulgaris</i> L.																							
<i>Veronica beccabunga</i> L.*	0.333									0.9					0.6								
<i>Veronica beccabunga</i> L.*										0.125		0.5											

Table 3 Means and standard deviations of physico-chemical data from the sampling stations. For the location of the sampling stations, see Fig. 1

	T°	[O ₂] mg L ⁻¹	pH	EC (µS cm ⁻¹)	[NO ₃ ²⁻] mg L ⁻¹	[NH ₄ ⁻] mg L ⁻¹	[PO ₄ ²⁻] mg L ⁻¹	[SiO ₂] mg L ⁻¹	[HCO ₃ ⁻] mg L ⁻¹	[SO ₄ ²⁻] mg L ⁻¹
RJO	15.3 ± 5.1	9.9 ± 1.5	8.2 ± 0.2	328 ± 36	3.7 ± 1.0	0.07 ± 0.04	0.03 ± 0.05	2.0 ± 0.8	149 ± 38	27.4 ± 6.8
ARD	19.4 ± 8.6	11.1 ± 2.2	8.3 ± 0.2	317 ± 35	2.0 ± 1.4	0.08 ± 0.06	0.01 ± 0.02	1.8 ± 0.6	139 ± 23	26.5 ± 6.5
ACH	15.1 ± 6.3	9.0 ± 4.5	7.9 ± 0.4	377 ± 71	1.3 ± 1.5	0.36 ± 0.58	0.01 ± 0.02	3.8 ± 1.8	181 ± 42	18.9 ± 7.0
GG3	16.1 ± 6.2	9.0 ± 1.3	7.8 ± 0.2	399 ± 111	12.4 ± 2.8	0.03 ± 0.03	0.02 ± 0.06	7.1 ± 1.2	207 ± 17	9.6 ± 0.6
GG2	16.3 ± 5.5	9.0 ± 1.3	7.8 ± 0.2	398 ± 111	12.3 ± 2.7	0.04 ± 0.03	0.02 ± 0.07	7.1 ± 1.3	210 ± 8	9.6 ± 0.6
GG1	16.3 ± 5.5	8.8 ± 1.1	7.8 ± 0.2	449 ± 60	13.0 ± 3.2	0.04 ± 0.03	0.02 ± 0.06	7.5 ± 1.2	212 ± 7	9.6 ± 0.6
ME2	14.3 ± 3.7	9.8 ± 1.8	7.7 ± 0.1	447 ± 60	10.0 ± 1.0	0.03 ± 0.03	0.00 ± 0.01	4.3 ± 0.9	224 ± 9	8.3 ± 1.6
ME3	12.9 ± 1.4	7.5 ± 1.0	7.6 ± 0.1	437 ± 49	8.1 ± 1.0	0.03 ± 0.04	0.00 ± 0.01	3.8 ± 0.7	220 ± 15	7.6 ± 3.1
LAU	12.3 ± 0.6	6.3 ± 1.0	7.4 ± 0.2	477 ± 37	12.9 ± 1.9	0.01 ± 0.02	0.01 ± 0.03	5.3 ± 3.0	238 ± 13	8.4 ± 0.9
ME4	13.7 ± 4.9	9.2 ± 2.4	7.6 ± 0.2	451 ± 49	8.2 ± 6.5	0.06 ± 0.05	0.00 ± 0.01	2.9 ± 1.4	231 ± 19	6.8 ± 1.2
SAU	13.0 ± 6.4	4.6 ± 3.6	7.5 ± 0.2	435 ± 95	0.3 ± 0.5	0.31 ± 0.30	0.05 ± 0.09	4.9 ± 2.4	242 ± 58	3.8 ± 2.0
MO1	12.6 ± 4.6	9.0 ± 2.7	8.1 ± 0.2	417 ± 38	3.2 ± 1.1	0.09 ± 0.10	0.01 ± 0.02	5.2 ± 4.0	215 ± 52	6.7 ± 1.8
MO2	13.1 ± 6.0	5.4 ± 3.9	7.6 ± 0.2	362 ± 82	0.3 ± 0.5	0.16 ± 0.13	0.01 ± 0.03	5.8 ± 4.8	198 ± 4	5.5 ± 3.1
MO3	12.8 ± 5.9	5.6 ± 4.7	7.6 ± 0.2	367 ± 115	0.1 ± 0.3	0.17 ± 0.16	0.00 ± 0.02	4.4 ± 2.4	201 ± 56	5.5 ± 5.8
MO4	12.4 ± 5.7	6.6 ± 4.1	7.7 ± 0.2	354 ± 103	0.1 ± 0.1	0.23 ± 0.30	0.01 ± 0.03	3.8 ± 2.2	189 ± 52	5.7 ± 5.6
VLO	12.0 ± 3.5	2.8 ± 2.0	7.5 ± 0.2	424 ± 41	1.3 ± 1.5	0.15 ± 0.14	0.02 ± 0.06	7.4 ± 1.6	193 ± 27	38.1 ± 10.1
EMC	15.0 ± 6.9	9.9 ± 4.3	7.8 ± 0.2	581 ± 74	3.8 ± 3.5	0.33 ± 0.27	0.11 ± 0.18	10.3 ± 4.1	289 ± 38	24.0 ± 3.9
LP3	15.0 ± 5.4	7.1 ± 1.4	7.6 ± 0.2	461 ± 103	11.4 ± 11.3	0.14 ± 0.12	0.01 ± 0.02	5.0 ± 3.8	209 ± 49	21.5 ± 5.6
LP2	16.1 ± 7.0	10.1 ± 2.2	8.0 ± 0.3	381 ± 89	3.9 ± 4.7	0.11 ± 0.07	0.01 ± 0.02	2.9 ± 3.0	167 ± 50	28.6 ± 5.8
LP1	15.3 ± 5.1	9.9 ± 1.5	8.2 ± 0.1	328 ± 36	3.7 ± 1.0	0.07 ± 0.04	0.03 ± 0.05	2.0 ± 0.8	149 ± 38	27.4 ± 6.8
ARG	17.1 ± 7.5	12.6 ± 3.4	8.5 ± 0.4	320 ± 93	1.5 ± 1.3	0.10 ± 0.06	0.01 ± 0.04	1.6 ± 0.7	118 ± 29	32.5 ± 3.3
RBR	13.3 ± 5.1	9.8 ± 1.8	8.2 ± 0.1	304 ± 33	2.6 ± 0.7	0.17 ± 0.07	0.05 ± 0.06	1.7 ± 0.6	122 ± 23	36.3 ± 5.8
RO3	12.8 ± 4.4	3.8 ± 2.0	7.5 ± 0.2	443 ± 58	0.7 ± 0.4	0.07 ± 0.04	0.01 ± 0.02	5.4 ± 1.6	210 ± 25	32.4 ± 4.5
RO2	12.3 ± 3.8	4.2 ± 1.7	7.6 ± 0.2	427 ± 49	0.6 ± 0.6	0.07 ± 0.05	0.00 ± 0.01	6.4 ± 1.5	197 ± 19	35.8 ± 4.6
RO1	12.3 ± 4.0	4.5 ± 1.0	7.7 ± 0.1	387 ± 59	1.5 ± 1.0	0.07 ± 0.05	0.02 ± 0.04	5.6 ± 2.2	176 ± 34	37.3 ± 4.0

in one of them, Fig. 4). Most of the species are very frequent (*Ceratophyllum demersum*, *Myriophyllum spicatum*, *Nuphar lutea*, *Phalaris arundinacea*, *Phragmites australis*). Some were abundant along the main river channel (*C. demersum*, *M. spicatum* and *P. arundinacea*). *Nuphar lutea* and *P. australis* were widely distributed in undisturbed wetlands (Pautou & Girel, 1981; Cernohous & Husak, 1986). *Potamogeton perfoliatus* occurred only in ACH, but this species also occurred along the main river channel. ACH was consequently close floristically to ARD, ARG and LPE. All these channels showed low species richness (from six for ARG, to eighteen for LPE).

LAU presented low species richness (only eleven species), although its water characteristics were similar to MEA. Of its species, 45% showed restricted distributions (in only two other channels, i.e. *Berula erecta*, *Hippuris vulgaris*, *Hottonia palustris*, *Juncus articulatus* and *Mentha aquatica*). All these species occurred in aquatic ecosystems supplied by mesotrophic groundwater (Bornette & Large, 1995), very infrequent in the Rhône River floodplain (Bornette *et al.* 1994c).

Three channels (VLO, MOR and ROS) contained widely distributed species, but also some infrequent or rare species. However, the latter were mostly helophytes or terrestrial species (*Epilobium* sp. and *Juncus effusus* in ROS, *Humulus lupulus*, *Lycopus europaeus* and *Rubus fruticosus* in VLO), also widely distributed in the floodplain. Thus, only *Riccia fluitans* and *Sagittaria sagittifolia*, occurring in MOR, were really rare, as they were not observed in the main river channel. These three channels showed intermediate species richness (respectively twenty-one, twenty-three and twenty-six species for VLO, ROS and MOR), with numerous hydrophytes in two of them (respectively thirteen and seventeen species in ROS and MOR).

SAU, MEA and GGR were characterized by numerous rare or sparsely distributed species. GGR showed the highest number of rare species (eleven) with the occurrence of *Chara major*, *Cladium mariscus*, *Juncus subnodulosus*, *Menyanthes trifoliata*, *Potamogeton friesii*, *P. coloratus*, *Ranunculus lingua*, *Thelypteris palustris*, *Typha latifolia*, *Alnus glutinosa* and *Utricularia minor*. *Alnus glutinosa* occurred in the inundated

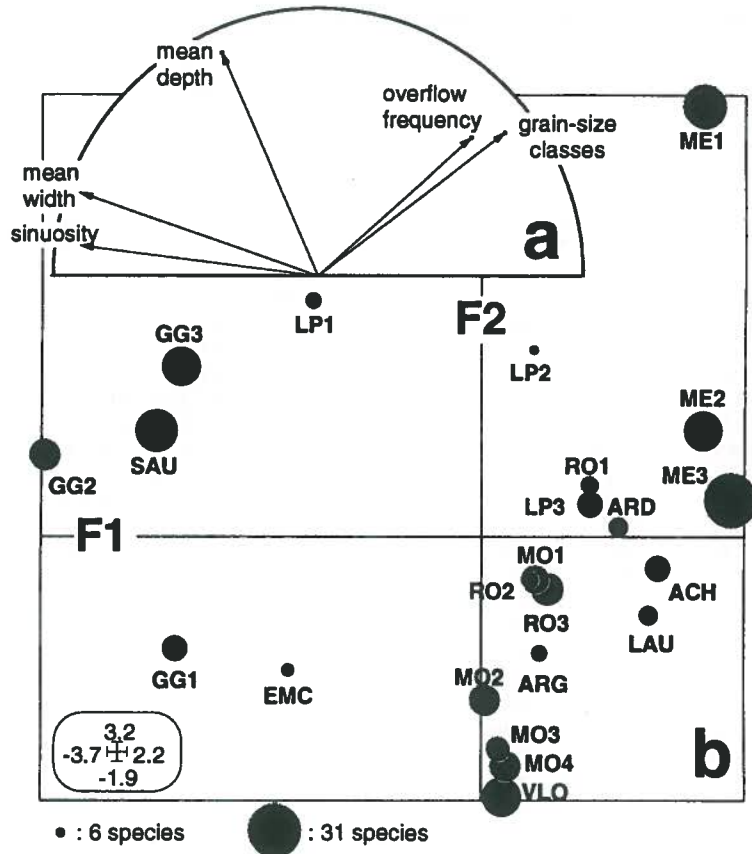


Fig. 2 Normalized PCA of environmental parameters. (a) Correlation circle of parameters with the first two axes of the analysis; (b) F1 × F2 factorial map of floristic zone coordinates on which species richness per floristic zone are plotted (circle sizes are proportional to species number). For code meaning and locations of floristic zones, see Fig. 1.

channel bed, but was frequently observed in the floodplain, and thus cannot be considered a rare species. *Chara major*, *Cladium mariscus*, *J. subnodulosus*, *P. coloratus* and *T. latifolia* have been observed in several cut-off channels supplied by groundwater of the Ain River, which is the largest tributary of the Rhône River upstream from Lyon (Bornette, Amoros & Rostan, 1996). *Menyanthes trifoliata*, *P. friesii*, *R. lingua*, *T. palustris* and *U. minor* occur nowhere else along the Rhône or the Ain River (Bornette *et al.*, 1996; G. Bornette, unpublished data). *Ranunculus lingua*, *Menyanthes trifoliata* and *T. palustris* occur only in a few sites in the surrounding mountainous regions, whereas *P. friesii* and *U. minor* occur sporadically in other aquatic ecosystems (Grenier, 1992; Bugnon *et al.*, 1993; Netien, 1993). *Ranunculus lingua* has frequently been found in the northern part of Europe (Johansson, 1993).

MEA showed the highest species richness (thirty-eight species) and was characterized by numerous rare or sparsely represented species (seven rare species,

six species occurred in only one other channel, and eleven occurred in two others). *Eleocharis acicularis*, *E. palustris*, *Fontinalis antipyretica*, *Glyceria fluitans*, *Luronium natans*, *Nitella confervacea* and *Senecio aquaticus* occurred only in MEA. *Eleocharis palustris* and *S. aquaticus* are frequent in ponds of the surrounding region (Netien, 1993). *Eleocharis acicularis*, *F. antipyretica*, *G. fluitans*, *L. natans* and *N. confervacea* grew permanently in this channel, and grow also in cut-off channels or in the main channel of the Ain River (Bornette *et al.*, 1996). *Luronium natans* occurs only in one site of the Ain River. *Berula erecta*, *C. vulgaris*, *H. palustris*, *J. articulatus*, *G. densa*, *Potamogeton natans* and *Ranunculus trichophyllus*, occurred in one or two other channels, and are usually found in groundwater-supplied ecosystems (Kohler *et al.*, 1974; Carbiener *et al.*, 1990). These species are also found in several cut-off channels of the Ain River (Bornette *et al.*, 1996).

SAU had intermediate species richness (twenty-four species) and few rare species (three), but numerous

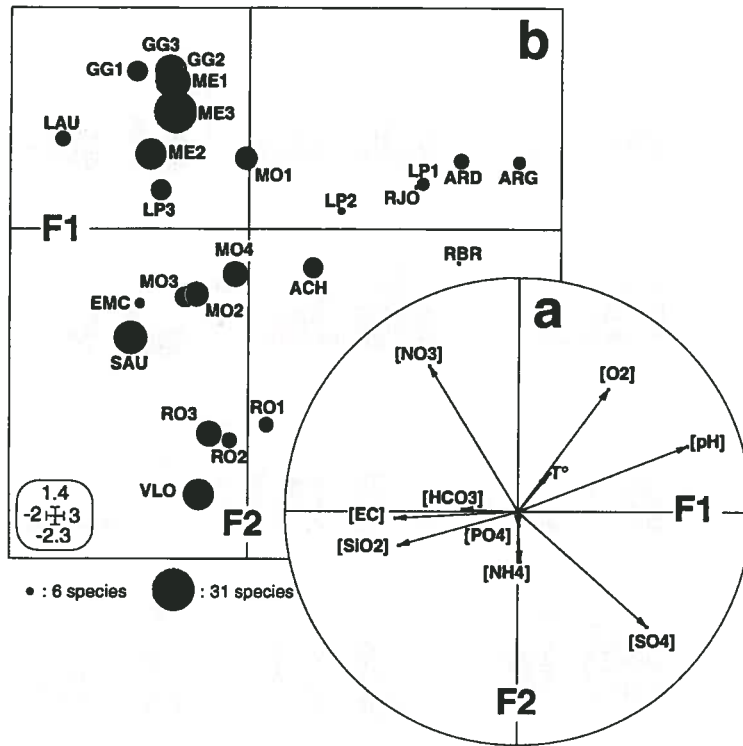


Fig. 3 Between-class nPCA (sampling stations as classes) of physico-chemical data set. (a) Correlation circle of physico-chemical parameters with the first two axes of the analysis; (b) F1 × F2 factorial map of station coordinates on which is plotted the species richness per floristic zone (circle sizes are proportional to the species number, and each station corresponds to one floristic zone). For code meaning and locations of sampling stations, see Fig. 1.

sparingly distributed species (eight species occurring only in one other channel, and three in two others). *Salix cinerea*, *Frangula alnus* and *Solanum dulcamara* occurred only in SAU, on the *Carex* floating mats, but were very common in the floodplain, and cannot therefore be considered rare. Most of the infrequent species (*Bidens tripartita*, *Carex pseudocyperus*, *Galium palustre*, *Hydrocharis morsus-ranae*, *Lysimachia vulgaris*, *Lythrum salicaria*, *Scrophularia auriculata*, *Scutellaria galericulata*, *Sparanium erectum* and *Urtica dioica*) were also widely distributed helophytes growing on floating mats. *Carex pseudocyperus* and *H. morsus-ranae* occurred only in one other channel, but were abundant in a large downstream tributary, the Saône River (G. Bornette, unpublished data).

Discussion

Previous studies in backwaters have shown that species richness is not simply related to the degree of connectivity to the main river channel through overflows (Lloyd & Walker, 1986; Roberts & Ludwig, 1991). Overflow frequency is an expression of connectivity that must be considered, together with the

geomorphology of channels, which may or may not allow flood-scouring of sediment and recruitment of new individuals (Henry, Amoros & Bornette, 1996).

Two cases were observed in which channels overflowed infrequently and possessed high sinuosity (low scouring) in relation to their groundwater connectivity (Fig. 5).

1 One channel (GGR) was isolated from the river, which for this reason could not supply any propagules (Fig. 2). High species richness results partly from its insularity. Numerous species occurring in this channel occur nowhere else in the floodplain, but are often observed in colder mountainous areas or in northern regions of Europe (Grenier, 1992; Bugnon *et al.*, 1993; Johannson, 1993; Netien, 1993). Other cases have been reported in which terrestrial plant species that usually occur in mountainous regions are also found in river floodplains (Pautou & Girel, 1986). They are probably species remaining from colder periods, saved from extinction by long-term isolation of the channel (disconnected from the river before 1649; Bravard, 1987) and by cold groundwater supplies (Fig. 3). Isolation probably prevents invasion by exotic species, and cold nutrient-poor groundwater supplies preclude com-

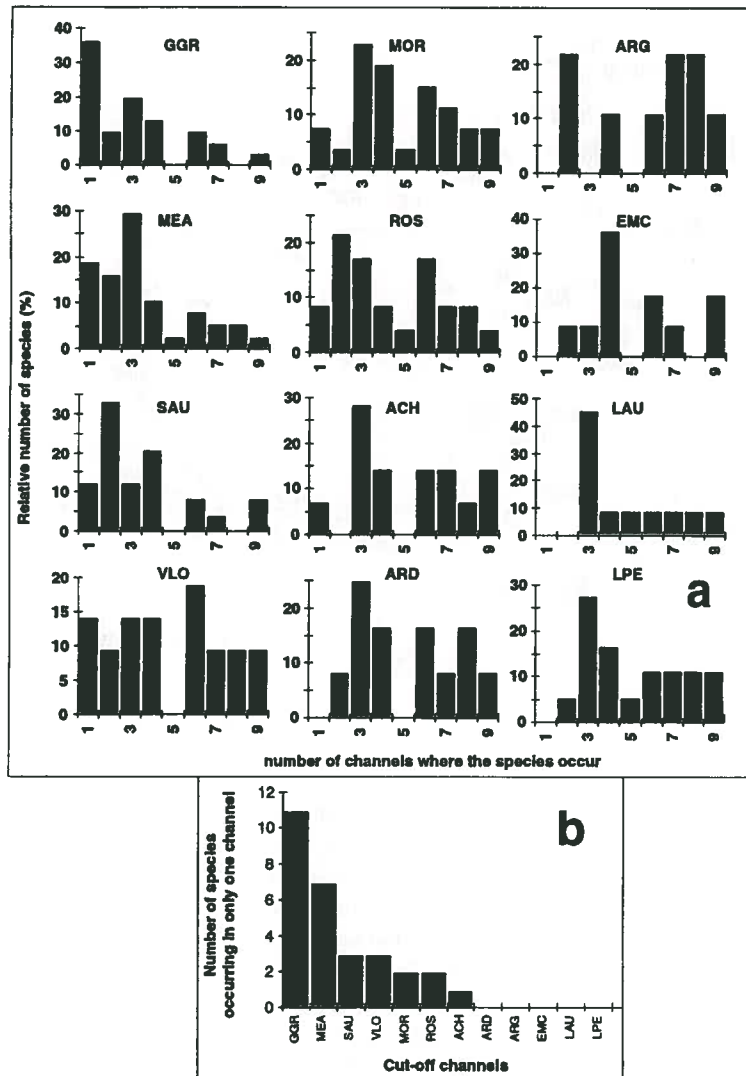


Fig. 4 Uniqueness of plant communities in each cut-off channel compared to the others. (a) Relative number of species in each channel (expressed as percentages of the channel species pool) belonging to each occurrence class (number of channels where the species occur; for further explanations, see text); (b) number of species occurring in only one channel (for channel abbreviations, see Table 1).

petition, maintaining favourable ecological conditions for the rare species. The large size of the ecosystem probably allows numerous microhabitats to co-occur, and permits more species to coexist (Grubb, 1977; Kohn & Walsh, 1994). However, species richness can only decrease, because any species extinction would not be compensated by the recruitment of new species entering this ecosystem through water fluxes. This probably explains the low hydrophyte richness of this ecosystem, as these species are usually transported by water fluxes, helophytes being more easily wind-dispersed (Cook, 1987).

2 Two other channels (SAU and EMC) were only

poorly supplied by hillslope groundwater (Figs 2 and 3) and presented intermediate-to-low species richness. In the species-poor EMC channel (eleven species), competitive processes should be intense, because of the absence of water renewal and also the small size of the ecosystem, both probably reducing the co-occurrence of diverse microhabitats. Propagules are probably rarely, if ever, brought to the channel, and Barrat-Segretain (1996) demonstrated that anchored hydrophyte species cannot be recruited because of a very deep layer of fluid organic matter that prevents any such recruitment. Thus, species richness can be expected to be low, in keeping with previous studies,

compensated for losses due to frequent flood scouring. Many frequently flooded cut-off channels supplied by nutrient-poor groundwater and located along the Ain River (flowing into the Rhône River just upstream from MEA) were a source of propagules and maintained fugitive species. In accordance with the intermediate disturbance hypothesis (Connell, 1978), high local instability (scoured patches) and high total stability (at channel level) of communities and of species richness were demonstrated by long-term investigations (Bornette *et al.*, 1994b; Barrat-Segretain & Amoros, 1996).

Surficial connectivity between riverine wetlands and a river cannot be reduced to a single phenomenon. Overflows of the river into cut-off channels bring nutrient-rich, fine sediments and propagules to the ecosystem, but water may be rapidly renewed by groundwater supplies. Sediments promote better recruitment of new individuals and/or species, and thus increase species richness. Conversely, river backflows maintain nutrient-rich and turbid water in the permanently connected downstream zone, impeding the recruitment of most propagules: a few species occur, and permanent connection reduces species richness.

The effects of connectivity depend on its nature (overflows vs. backflows, hillslope vs. seepage groundwater), its intensity (permanent connection, vs. rare overflows), and geomorphological characteristics of the channels (low sinuosity, and higher scouring ability of floods vs. high sinuosity, and low scouring). High surficial connectivity decreases species richness and occurrence of rare species, but overflows enhance biodiversity to some extent, depending on the occurrence of propagule pools at the river landscape level. In many wetlands, changes in connectivity, or the exhaustion of propagule pools, should lead to a decrease in species richness.

The effects of connectivity appear much more complex than previously hypothesized. However, their understanding can explain patterns of richness and rarity observed in riverine wetlands, and permit us to forecast community dynamics and thus guidelines for the conservation of this biodiversity.

Acknowledgements

We gratefully acknowledge the assistance of M.H. Barrat-Segretain for valuable discussions on the manu-

script, two anonymous reviewers for improving a previous version of the paper, and T. Partrick for providing linguistic assistance. This study was part of the 'DSPT5 Biodiversity Action' founded by the French Ministère de l'Enseignement Supérieur et de la Recherche.

References

- Amoros C. (1991) Changes in side-arm connectivity and implications for river system management. *Rivers*, **2**, 105–112.
- Amoros C. & Roux A.L. (1988) Interactions between water bodies within the floodplains of large rivers, function and development of connectivity. *Münstersche Geographische Arbeiten*, **29**, 125–130.
- Barko J.W. & Smart R.M. (1986) Sediment-related mechanisms of growth limitation in submersed macrophytes. *Ecology*, **67**, 1328–1340.
- Barrat-Segretain M.H. (1996) Germination and colonization dynamics of *Nuphar lutea* L. in a former river channel. *Aquatic Botany*, **55**, 31–38.
- Barrat-Segretain M.H. & Amoros C. (1996) Recovery of riverine vegetation after experimental disturbance, a field test of the Patch Dynamics Concept. *Hydrobiologia*, **321**, 53–68.
- Bornette G. & Amoros C. (1991) Aquatic vegetation and hydrology of a braided river floodplain. *Journal of Vegetation Science*, **2**, 497–512.
- Bornette G. & Large A.R.G. (1995) Groundwater-surface water ecotones at the upstream part of confluences in former river channels. *Hydrobiologia*, **310**, 123–137.
- Bornette G., Amoros C. & Chessel D. (1994a) Effect of allogenic processes on successional rates in former river channels. *Journal of Vegetation Science*, **5**, 237–246.
- Bornette G., Amoros C., Castella C. & Befly J.L. (1994b) Succession and fluctuation in the aquatic vegetation of two former Rhône River channels. *Vegetatio*, **110**, 171–184.
- Bornette G., Henry C., Barrat M.H. & Amoros C. (1994c) Theoretical habitat templates species traits and species richness, aquatic macrophytes in the Upper Rhône River and its floodplain. *Freshwater Biology*, **31**, 487–505.
- Bornette G., Amoros C. & Rostan J.C. (1996) River incision and decennial vegetation dynamics in cut-off channels. *Aquatic Sciences*, **58**, 31–51.
- Braun-Blanquet J. (1932) *Plant Sociology, the Study of Plant Communities*. Translated by G. D. Fuller and H. S. Conard. McGraw Hill Book Co., New York, NY.
- Bravard J.P. (1987) *Le Rhône du Léman à Lyon*. La Manufacture (ed.), Lyon.
- Bravard J.C. & Gilvear D.J. (1993) Structure hydro-

- géomorphologique des hydrosystèmes. *Hydrosystèmes Fluviaux* (eds C. Amoros and G. Petts), pp. 83–103. Masson, Paris.
- Bravard J.P., Amoros C. & Pautou G. (1986) Impact of civil engineering works on the successions of communities in a fluvial system. *Oikos*, **47**, 92–111.
- Bravard J.P., Amoros C., Pautou G., Bornette G., Bournaud M., Creuzé des Châtelliers M., Gibert J., Peiry J.L., Perrin F. & Tachet H. (1997) Stream incision in Southeast France, morphological phenomena and impacts upon biocenoses. *Regulated Rivers*, **13**, 75–90.
- Bugnon F., Felzines J.C., Loiseau J.E. & Royer J.M. (1993) *Nouvelle Flore de Bourgogne. Tome I. Catalogue Général et Fichier Bibliographique*. Bulletin Scientifique de Bourgogne, Dijon.
- Carbiener R., Trémolières M., Mercier J.L. & Ortscheit A. (1990) Aquatic macrophyte communities as bioindicators of eutrophication in calcareous oligosaprobe stream waters (Upper Rhine plain Alsace). *Vegetatio*, **86**, 71–88.
- Carpenter S.R. (1981) Submersed vegetation, an internal factor in lake ecosystem succession. *American Naturalist*, **118**, 372–383.
- Cellot B., Dole-Olivier M.J., Bornette G. & Pautou G. (1994) Temporal and spatial environmental variability in the Upper Rhône River and its floodplain. *Freshwater Biology*, **31**, 311–326.
- Cernohous F. & Husak S. (1986) Macrophyte vegetation of Eastern and North-eastern Bohemia. *Folia Geobotanica Phytotaxonomica*, **21**, 1–112.
- Connell J.H. (1978) Diversity in tropical rain forest and coral reefs. *Science*, **199**, 1302–1310.
- Cook C.D.K. (1987) Dispersion in aquatic and amphibious vascular plants. *Plant Life in Aquatic and Amphibious Habitats* (ed. R. M. M. Crawford), pp.179–190. Special Publication No. 5 of the British Ecological Society, Blackwell Scientific Publications, Oxford.
- Dolédec S. & Chessel D. (1991) Recent developments in linear ordination methods in environmental sciences. *Advances in Ecology*, **1**, 133–155.
- Drago E.C. (1976) Origen y clasificacion de ambientes leníticos en llanuras aluviales. *Revista Asociacione Ciencias Naturales Literarias*, **7**, 123–137.
- Foeckler F., Diepolder U. & Deichner O. (1991) Water mollusc communities and bioindication of Lower Salzach floodplain waters. *Regulated Rivers*, **6**, 301–312.
- Goodall D.W. (1954) Objective methods for the classification of vegetation. III An essay in the use of factor analysis. *Australian Journal of Botany*, **2**, 304–324.
- Grenier E. (1992) *Flore d'Auvergne*. Edition de la Société Linnéenne de Lyons, Lyons.
- Grubb P.J. (1977) The maintenance of species-richness in plant communities, the importance of the regeneration niche. *Biological Review*, **52**, 107–145.
- Henry C., Amoros C. & Bornette G. (1996) Species traits and recolonization processes after flood disturbance in riverine macrophytes. *Vegetatio*, **122**, 13–27.
- Holcik J., Bastl I., Ertl M. & Vranovsky M. (1981) Hydrobiology and ichthyology of the Czechoslovak Danube in relation to predicted changes after the construction of the Gabčíkovo-Nagymaros river barrage system. *Práce Laboratória Rybárstva a Hydrobiologie*, **3**, 19–158.
- Johannson M.E. (1993) Factors controlling the population dynamics of the clonal helophyte *Ranunculus lingua*. *Journal of Vegetation Science*, **4**, 621–632.
- Juget J., Yi B.J., Roux C., Richoux P., Richardot-Coulet M., Reygrobellet J.L. & Amoros C. (1979) Structure et fonctionnement des écosystèmes du Haut Rhône français. VII. Le complexe hydrographique de la Lône des pêcheurs (un ancien méandre du Rhône). *Schweizerische Zeitschrift für Hydrologie*, **41**, 395–417.
- Keddy P.A. (1983) Shoreline vegetation in Axe Lake Ontario, effects of exposure on zonation patterns. *Ecology*, **64**, 331–344.
- Kohler A., Brinkmeier R. & Vollrath H. (1974) Verbreitung und Indikatorwert der submersen Makrophyten in den Fließgewässern der Friedberger Au. *Bericht der Bayerischen botanischen Gesellschaft zur Erforschung der heimischen Flora*, **45**, 5–36.
- Kohn D.D. & Walsh D.M. (1994) Plant species richness—the effect of island size and habitat diversity. *Journal of Ecology*, **82**, 367–377.
- Lamberti G.A., Gregory S.V., Ashkenas L.R., Wildman R.C. & Moore K.M.S. (1991) Stream ecosystem recovery following a catastrophic debris flow. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 196–207.
- Lloyd L.N. & Walker K.F. (1986) Distribution and conservation status of small freshwater fish in the river Murray South Australia. *Transactions of the Royal Society of South Australia*, **110**, 49–57.
- Macan T.T. (1977) Changes in the vegetation of a moorland fishpond in twenty-one years. *Journal of Ecology*, **65**, 95–106.
- Martinet F., Juget J. & Riera P. (1993) Carbon fluxes across water sediment and benthos along a gradient of disturbance intensity, adaptive responses of the sediment feeders. *Archiv für Hydrobiologie*, **127**, 19–56.
- Netien G. (1993) *Flore Lyonnaise*. Edition de la Société Linnéenne de Lyons, Lyons.
- Nilsson C., Gardfjell M. & Grelsson G. (1991a) Importance of hydrochory in structuring plant communities along rivers. *Canadian Journal of Botany*, **69**, 2631–2633.
- Nilsson C., Grelsson G., Dynesius M., Johannson M.E. &

- Sperens U. (1991b) Small rivers behave like large rivers, effect of postglacial history on plant species richness along riverbanks. *Journal of Biogeography*, **18**, 533–541.
- Ortscheit A. (1985) Evolution de la végétation aquatique du Waldrhein près de Strasbourg un ancien bras du Rhin à status hydrologique original. *Bulletin de l'Association Philomatique d'Alsace-Lorraine*, **21**, 195–237.
- Pautou G. & Girel J. (1981) Les associations végétales à *Cladium mariscus* dominant dans la vallée du Rhône entre Lyons et Genève. *Colloques Phytosociologiques*, **10**, 333–349.
- Pautou G. & Girel J. (1986) La végétation de la basse plaine de l'Ain: organisation spatiale et évolution. *Documents de Cartographie Ecologique*, **29**, 75–96.
- Petts G. & Amoros C. (eds) (1996) *Fluvial Hydrosystems*. Chapman & Hall, London.
- Poff N.L. & Ward J.V. (1990) Physical habitat template of lotic systems, recovery in the context of historical pattern of spatiotemporal heterogeneity. *Environmental Management*, **14**, 629–645.
- Reygrobelle J.L., Mathieu J., Ginet R. & Gibert J. (1981) Structure et fonctionnement des écosystèmes du Haut-Rhône français; VIII, Hydrologie de deux stations phréatiques dont l'eau alimente des bras-morts. *International Journal of Speleology*, **11**, 129–139.
- Roberts J. & Ludwig J.A. (1991) Riparian vegetation along current-exposure gradients in floodplain wetlands of the River Murray, Australia. *Journal of Ecology*, **79**, 117–127.
- Rostan J.C., Amoros C. & Juget J. (1987) The organic content of the surficial sediment, a method for the study of ecosystems development in abandoned river channels. *Hydrobiologia*, **148**, 45–62.
- Schneider R.L. & Sharitz R.R. (1988) Hydrochory and regeneration in a bald cypress-water tupelo swamp forest. *Ecology*, **69**, 1055–1063.
- Thioulouse J., Dolédec S., Chessel D. & Olivier J.M. (1995) ADE Software, multivariate analysis and graphical display of environmental data. *Software per l'ambiente* (eds G. Guariso and A. Rizzoli), pp. 57–62. Pàtron editore, Bologna.
- Trémolières M., Carbiener D., Carbiener R., Eglin I., Robach F., Sanchez-Pérez J.M., Schnitzler A. & Weiss D. (1991) Zones inondables, végétation et qualité de l'eau en milieu alluvial rhénan, l'île de Rhinau un site de recherches intégré. *Bulletin d'Ecologie*, **22**, 317–336.
- Ward J.V. & Stanford J.A. (1995) Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. *Regulated Rivers*, **11**, 105–119.
- Wetzel R.G. (1979) The role of the littoral zone and detritus in lake metabolism. *Archiv für Hydrobiologie*, **13**, 145–161.
- Whittaker R.H. & Levin S.A. (1977) The role of mosaic phenomena in natural communities. *Theoretical Population Biology*, **12**, 117–139.
- Wisheu I.C. & Keddy P.A. (1991) Seed banks of a rare wetland plant community, distribution pattern and effect of human-induced disturbance. *Journal of Vegetation Science*, **2**, 181–188.

(Manuscript accepted 29 September 1997)