Ecological complexity of wetlands within a river landscape

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Abstract

The sustainable conservation of diversity in riverine wetlands implies knowledge of the basic geomorphological and ecological processes that inter play at the landscape scale. Eight hypothetical types of wetlands, predicted as differing in their plant communities, were proposed by combination of three factors (geomorphological pattern, river incision vs aggradation, groundwater origin), selected because they determine the effects of flood disturbances (intensity, frequency) and the water supplies. This hypothesis was tested through the comparison of the vegetation and the physico-chemistry of cut-off channels of the Ain River in France. Cut-off meanders were related to meso-eutraphent plant species of standing water, aggraded meanders being more frequently overflowed than incised ones. Braided channels were characterized by flood-tolerant species, some of the incised ones being related to oligotraphent communities, but some remaining connected, through seepage and floods, to the river (mesotraphent species). The ratio of side-hill aquifer to seepage supplying these channels depends on river vs aquifer levels but also on their elevation from the river level, determined by their age. The study demonstrates the effect of geomorphology and of water supplies on floristic assemblages, but some other features must also be considered. The high diversity of functioning implies that conservation of such ecosystems should consider all the parts of the river landscape and all the processes that interfere on several time-scales. © 1998 Elsevier Science Ltd. All rights reserved

1. Introduction

The river floodplains are often characterized by numerous wetlands that result from both river dynamics (e.g. lateral erosion, changes in river course) and ecological successions that have proceeded in the cut-off channels (Drago, 1976; Bravard et al., 1986; Salo et al., 1986; Kalliola et al., 1991). It has been demonstrated that riverine wetland ecosystems are a major source of diversity in terms of habitats and communities (Kalliola and Puhakka, 1988; Castella et al., 1991; Copp, 1991; Bornette et al., 1994a). The maintenance of this diversity requires a knowledge of the processes responsible.

Aquatic communities, and particularly aquatic macrophytes, are determined by nutrient levels that are ruled by the different water fluxes occurring in these

ecosystems (Kohler et al., 1974; Kohler and Schiele, 1985; Ortscheit, 1985; Carbiener et al., 1990). These fluxes include groundwater supplies coming from: (1) the hillslope aquifer; (2) seepage from the river filtering in and out of the cut-off channels; and (3) surface water supplies through backflows of river in the cut-off channels as well as river overflows (Juget et al., 1979; Grootjans, 1985; Kohler and Schiele, 1985; Wassen et al., 1990; Trémolières et al., 1991).

Flood disturbances act also in the dynamics of such ecosystems. Studies have demonstrated that aquatic macrophytes are able to delineate the intensity and frequency of flood disturbances (Bornette et al., 1994a, b). These disturbances depend mainly on the geomorphological pattern of the river (Leopold and Wolman, 1957; Church, 1992), and its aggradation or incision (Galay, 1983, Bravard, 1994; Bravard et al., 1997). The geomorphology determines its bedform (cross-section, sinuosity, slope), and thereby the flow velocity, and the

intensity of the scouring effect of floods (Bravard et al., 1986; Amoros et al., 1987). The incision is the progressive deepening of the main river, whereas the aggradation is the opposite phenomenon due to the accumulation of coarse sediment that leads to the elevation of the river channel (Galay, 1983; Bravard, 1994). Incision leads to the progressive isolation of the river from its floodplain (Foeckler et al., 1991, 1994; Babinski, 1992; Bornette and Heiler, 1994), and consequently decreases the flood frequency and seepage supply to the riverine wetlands (Galay, 1983; Petts, 1984; Bravard and Petts, 1993; Bravard, 1994; Foeckler et al., 1994; Landon and Piegay, 1994; Reich, 1994).

In the floodplains of rivers flowing from alpine areas (piedmont rivers), the aquifers have been demonstrated to be highly connected to the cut-off channels (Reygro-bellet and Castella, 1987; Trémolières et al., 1991; Malanson, 1993; Stanford and Ward, 1993). These cut-off channels can be ranged on a gradient of nutrient content of the water because they can be supplied by river seepage and groundwater from the hill-side aqui-fer. Seepage is usually richer in nutrients because of the supply of human effluents to the main river channel, and may supply the braided cut-off channels that are closer to the river, as well as those located in the aggrading sectors (Bornette et al., 1994c, b; Bravard et al., 1997). Conversely, the hill-side aquifer is frequently nutrient poor, and could differ in nutrient content on the two sides of the alluvial plain, depending on the surrounding land uses (Bornette and Amoros, 1991). This aquifer may preferentially supply cut-off channels located in the incised reaches.

Studies on the functioning of cut-off channels usually consider these processes independently, but for biological conservation we need to consider the interactions between all these processes. The combination of these variables produces eight hypothetical types of riverine wetlands, predicted as differing in their aquatic plant communities (Fig. 1). The present paper aims to test this hypothesis through the comparison of the aquatic plant communities occurring in the cut-off channels of the lower Ain River near Lyon in South-East France.
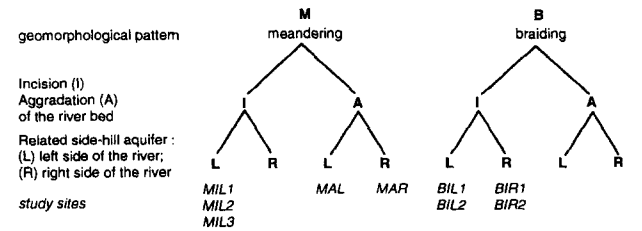

Fig. 1. Predicted typology of river cut-off channels based on their main geomorphological and environmental characteristics. Each study site is labelled by a code: M vs B as Meander vs Braided; I vs A as Incision vs Aggradation, and L vs R as Left vs Right side of the river (for their location, see Fig. 2).

2. Study sites

The comparison of the aquatic plant communities was carried out on a floodplain section of the Ain River, that includes nine cut-off channels disconnected from the river at their upstream end (Fig. 2). These channels differ in their geomorphology and occur in either an incised or an aggraded sector (during the 1976–1986 period). Their geomorphology and their location (right or left side of the river), allows one to distinguish five groups within the eight hypothetical cases listed in Fig. 1.

3. Material and methods

3.1. Physico-chemistry of the water

Water samples were collected for chemical analysis on 11 occasions over 2 years in the nine channels and the
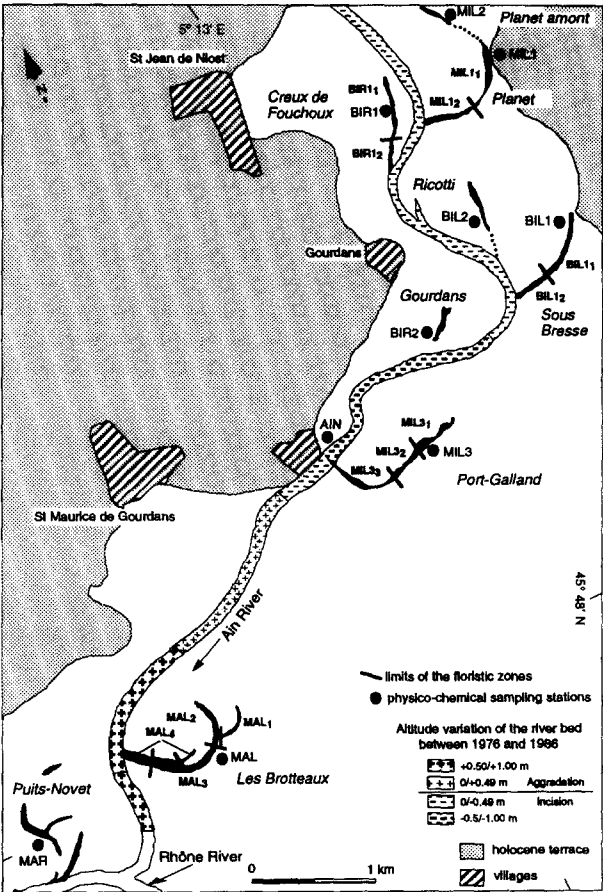
Fig. 2. Location of the nine studied cut-off channels in the alluvial floodplain of the Ain River. The location of the floristic zones and the chemical sampling stations are indicated along each channel, as well as the coded labels used in the others figures and in the text. For the code meaning, see Fig. 1; code indices indicate the floristic zones within each channel. Aggradation (+) or incision (−) of the river reaches in the channel areas are indicated directly on the river sections where they have been measured.

main river (Fig. 2; sampling dates: March, April, May and June 1994, and April, May, June, July, August, October, and December 1995). They were brought to the laboratory in an ice box, stored at 4°C and analysed the day after.

Nitrate N, Ammonium N, Sulphate, Phosphate and Silica contents were measured by colorimetry after standard HACH procedures (HACH Company, PO Box 389 Loveland, CO). Alkalinity was measured by HCl N/10, conductivity, water temperature, oxygen concentration and pH were measured in situ with MERCK meters. Higher values of conductivity, alkalinity and silica contents indicate supplies of groundwater to the cut-off channels (Bornette and Amoros, 1991; Bornette and Large, 1995). Groundwater is also usually characterized by high nitrate content (Bornette and Amoros, 1991; Bornette et al., 1996a). Phosphate, ammonia and nitrate contents also provide information on farmland sewage drainage. High pH values frequently indicate river water or seepage (Juget et al., 1979; Bornette and Amoros, 1991; Bornette and Large, 1995). Average physico-chemical values measured in the stations are indicated in Table 1

3.2. Aquatic vegetation

The aquatic vegetation was surveyed during July 1992, in 2 m-wide sampling plots regularly distributed along the cut-off channels: 16 plots along Planet (MIL1), 10 along Planet amont (MIL2), 33 along Port-Galland (MIL3), 43 along Brotteaux (MAL), 22 along Puits-Novet (MAR), 14 along Sous-Bresse (BIL1), nine along Ricotti (BIL2), 21 along Creux de Fouchoux (BIR1), and six along Gourdans (BIR2). The vegetation was recorded using the double Braun-Blanquet (1932) cover and sociability scale, which was converted into a single value for multivariate statistical analyses (Balocco-Castella, 1988; Bornette and Amoros, 1991).

The floristic data consisted of 174 sampling plots with 99 species (Table 2).

3.3. Data analysis

The physico-chemical dataset was analysed by between-class normalised Principal Component Analysis (nPCA) using the ADE package version 4.0 (Chessel and Dolédec, 1996), the sampling stations being considered as classes (Dolédec and Chessel, 1989, 1991). Data were normalised then averaged per sampling station. This reduced data set was then analysed by simple nPCA. This analysis focused on the mean differences between the sampling stations.

Likewise, the floristic data set was analysed using (1) simple centred Principal Component Analysis (cPCA), (Goodall, 1954; Orloci, 1966), and (2) a between-class cPCA (each floristic zone or each channel being considered as a class). The first analysis (cPCA) provides the floristic zonation of each channel: these zones have been demonstrated to be an appropriate spatial scale for investigations in cut-off channels (Bornette et al., 1994c, 1996a). The second analysis permitted comparison of the floristic differences among floristic zones (zones as classes) or channels (channels as classes) considered as a whole.

4. Results

4.1. Physico-chemical data

The first two axes of the nPCA contributed 79 and 12% respectively of the total variation. Three incised sites (MIL1, MIL2 and BIL1) had negative values on the F1 axis (Fig. 3(a)) and were related to the highest conductivity, alkalinity, nitrate, silica and phosphate contents. This indicates that they are supplied principally

Table 1

Average values of physico-chemical parameters (mean ± SD) in the sampling stations. Station codes are explained in Fig. 1 and their locations shown in Fig. 2

Station	Temperature °C	[O₂] %	pH	EC (μS cm⁻¹)	[N–NO₃] (mg l⁻¹)	[N–NH₄] (mg l⁻¹)	[P–PO₄] (mg l⁻¹)	SiO₂ (mg l⁻¹)	[HCO₃⁻] (mg l⁻¹)
MIL1	14·2 ± 3·2	84 ± 14	7·5 ± 0·2	494 ± 62	4·2 ± 0·8	0·11 ± 0·11	0·11 ± 0·09	8·2 ± 2	236 ± 18
MIL2	12·2 ± 2·6	73 ± 10	7·6 ± 0·2	495 ± 37	2·8 ± 0·9	0·06 ± 0·08	0·10 ± 0·07	7·9 ± 3·5	243 ± 18
MIL3	15·9 ± 5·4	88 ± 19	7·6 ± 0·2	398 ± 25	0·9 ± 0·3	0·05 ± 0·05	0·04 ± 0·04	5·6 ± 1·4	211 ± 14
MAL	13·2 ± 4·2	69 ± 18	7·7 ± 0·1	376 ± 33	0·4 ± 0·4	0·04 ± 0·04	0·04 ± 0·05	3·9 ± 1·4	194 ± 21
MAR	14·3 ± 5·3	86 ± 21	7·7 ± 0·4	343 ± 31	0·5 ± 0·3	0·04 ± 0·06	0·02 ± 0·01	3·2 ± 0·9	186 ± 10
BIL1	14 ± 3	65 ± 12	7·4 ± 0·1	537 ± 43	5·4 ± 1·5	0·04 ± 0·04	0·10 ± 0·08	9·4 ± 1·3	240 ± 11
BIL2	13 ± 4·2	66 ± 10	7·6 ± 0·1	399 ± 27	0·7 ± 0·3	0·07 ± 0·10	0·03 ± 0·03	6·2 ± 2	213 ± 15
BIR1	14·5 ± 4·8	75 ± 14	7·7 ± 0·3	348 ± 36	0·7 ± 0·3	0·04 ± 0·05	0·04 ± 0·04	3·8 ± 1·4	187 ± 12
BIR2	14·4 ± 4·1	82 ± 17	7·7 ± 0·2	409 ± 34	0·7 ± 0·3	0·06 ± 0·06	0·04 ± 0·04	6·2 ± 1·8	215 ± 15
AIN	13·6 ± 4·2	105 ± 14	8·2 ± 0·2	354 ± 29	0·8 ± 0·2	0·05 ± 0·06	0·05 ± 0·04	3·5 ± 1·1	188 ± 10
Left-side aquifer				510 ± 64	4·2 ± 1·3				
River aquifer				394 ± 14	2·7 ± 0·2				

Table 2

Species recorded in nine channels of the Ain River. The names of the species are related to their abbreviations used in figures and are followed by the mean abundance of the species in each channel or floristic zone. For the abbreviations of the channels, see Fig. 2. Nomenclature follows Lambinon et al. (1992)

Abbr	Name	MIL1$_1$	MIL1$_2$	MIL2	MIL3$_1$	MIL3$_2$	MIL3$_3$	MAL$_1$	MAL$_2$	MAL$_3$	MAL$_4$	MAR	BIL1$_1$	BIL1$_2$	BIL2	BIR1$_1$	BIR1$_2$	BIR2
Ach	*Achillea ptarmica*	0	0	0	0	0	0	0	0	0	0·11	0·64	0	0	0	0	0	0
Agr	*Agrostis canina*	0	0	0	0	0	0	0	0·29	0	0·56	0·77	0	0	0	0	0	0·83
Apl	*Alisma plantago-aquatica*	0·11	0·57	0	0·31	0·2	0	0	0·24	0·25	0·22	0·45	0·44	0	0·33	0·08	0·13	0·33
Ara	*Alisma ranunculoides*	0	0	0	0	0	0	0	0	0	0	0·14	0	0	0	0	0	0
Aln	*Alnus glutinosa*	0	0	0·3	0	0	0	0	0	0	0	0·09	0	0·6	0	0	0	0
Ber	*Berula erecta*	0·56	3·43	1	0	0·8	0·1	0·22	1·29	0·75	0·78	0·05	1·11	3·2	1·89	1·38	2·0	2·83
Cal	*Callitriche platycarpa*	0	3·43	0	0	0	0·1	0·11	0·24	1·25	0·78	0·32	0	1·6	0·78	1·0	2·38	0·67
Cse	*Calystegia sepium*	0·44	0	0	0	0	0	0·67	0·18	0·13	0·22	0·32	0	0·6	0·22	0	0	0
Cac	*Carex acutiformis*	0	0	0	0	0	0	0	0·47	0	0	0·05	0	0	0	0	0	0
Cel	*Carex elata*	3·33	2·86	5·1	2	2·1	2·6	4·44	4·41	2	2·89	0·5	0·78	3·0	1·44	1·0	1·25	3·00
Cfl	*Carex flava*	0	0	0·4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cer	*Ceratophyllum demersum*	0·11	1·71	0	0·15	0	4·4	0	0	0·38	0	0·14	0	0	0	0	0·13	0
Cas	*Chara aspera?*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0·33
Cma	*Chara major*	0	0	1·3	0	2·9	0	0	0	0	0	0	2·89	4·2	2	0	0	2·5
Cvu	*Chara vulgaris*	0	0	0·3	0·54	0	0	0·11	0·76	0	0	0·09	0	0	0·67	0	0	0
Cir	*Cirsium arvense*	0	0	0	0	0	0	0·22	0	0	0·22	0·09	0	0	0	0	0	0
Cla	*Cladium mariscus*	0	0	3·2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cra	*Crataegus monogyna*	0	0	0	0	0	0	0·11	0·06	0	0	0	0	0	0	0	0	0
Des	*Deschampsia cespitosa*	0	0	0	0	0	0	0	0	0	0	0·27	0	0	0	0	0	0
Eac	*Eleocharis acicularis*	0·22	0	0	0	0	0	0	0·41	0	0	0	0	0	0·56	0·08	0	1·33
Epa	*Eleocharis palustris*	0	0	0	0	0	0·3	0	0·22	0	0	0	0	0	0	0	0	0
Elo	*Elodea canadensis*	0	3·71	0	0	0	0·7	0	0	3·75	0	0·05	0·56	0	0·44	0·62	4	0·67
Equ	*Equisetum fluviatile*	0	0·71	0	0	0·4	0·2	0	2	0	0	0	0	0	0·11	0	0·13	0
Fil	*Filipendula ulmaria*	0	0	0	0·15	0	0	0	0·12	0	0	0	0	0	0	0	0	0
Fon	*Fontinalis antipyretica*	0	0	0	0	0	0	0	0·24	0	0	0	0	0	0	0·15	0	0
Fra	*Fraxinus excelsior*	0	0	0	0·8	0	0	0	0	0	0	0·05	0	0·8	0	0	0	0
Gal	*Galium palustre*	1·33	1·71	0	0·15	0·1	0	1·33	0·88	0·38	2·11	0·77	0·22	0·6	0·56	0	0	0·83
Gly	*Glyceria fluitans*	0	0	0	0	0	0	0	0·71	1·25	0	0	0	0	0	0	0	0
Gro	*Groenlandia densa*	0	1·71	0·1	0	0	0·2	0	0·94	1	0	0·27	0·44	0	0·11	0	0·25	2·67
Hip	*Hippuris vulgaris*	0	0·71	0	0	0	0·7	0	0·65	2·75	0·44	0	0	0·8	0·33	0	0·25	1
Hot	*Hottonia palustris*	0·56	0·71	0	0·85	0·2	0·6	0	0·06	1·25	0	0	0	0·6	0·56	0	0	0·33
Hum	*Humulus lupulus*	0	0	0	0	0	0	0·11	0	0	0	0·32	0	0	0	0	0	0
Iri	*Iris pseudacorus*	0·56	0	0·6	0·54	0·4	0	2·11	0·47	0	1	0·05	0·22	0	0·33	0	0·25	1
Jar	*Juncus articulatus*	0	0	1·5	0	1·9	0	0·11	2·59	0	0·33	0	3·11	1	0·78	0·08	0·25	3·67
Ltr	*Lemna trisulca*	0	0	0	0	0	0	0	0	0	0	0·05	0	0	0	0	0	0
Lud	*Ludwigia palustris*	0	0	0	1	0·4	0·8	0	0	0	0	0	0·11	0·4	0	0	0	0
Lyc	*Lycopus europaeus*	0·11	0	0·1	0	0·1	0	0	0·18	0	0·33	0	0	0	0·11	0	0	0
Lnu	*Lysimachia nummularia*	0	0	0	0	0	0	0	0	0	0	0	0	0	0·33	0	0	0
Lvu	*Lysimachia vulgaris*	0·89	0	0·6	0·38	0·5	0	0·89	0·29	0·38	1·22	0	0	1·2	0·22	0	0	0·17
Lyt	*Lythrum salicaria*	1	0·29	0·5	0·23	1	1·3	0·56	0·65	1·75	1·67	1·18	0·11	0·8	0	0·15	0	0·33
Men	*Mentha aquatica*	1·11	1·29	2·2	0·08	1·1	0·2	1·56	2·88	0·38	3·56	0·82	2	3	1·56	0·77	0	2·17
Myo	*Myosotis scorpioides*	0·67	1·86	0·3	0	0·2	0	0	1	1·25	1	0·45	0·33	0	0·22	0·46	0·75	0·33
Msp	*Myriophyllum spicatum*	0	0	0	2·23	0·3	2·1	0	0	1·38	0	1·45	0	0	0	0·08	0·75	0·33
Mve	*Myriophyllum verticillatum*	4·33	0·43	0·3	4·69	0·6	1·5	0	0·65	0·38	0	0·09	0	0·4	0·44	0·15	0·63	1·33
Nas	*Nasturtium officinale*	0	0	0	0	0·6	0	0	0	0	0	0	0	0	0	0	0	0
Ngr	*Nitella gracilis*	0	0	0	0	0	0·4	0	0	0	0	0	0	0	0	0	0	0
Nsy	*Nitella syncarpa*	0	0	0	0·31	0	0	0	0·18	0	0	0	0·44	0	0	0	0	0·83
Nte	*Nitella tenuissima*	0	0	0	0·54	0	0	0	0	0	0	0	0	0	0	0	0	0
Nup	*Nuphar lutea*	2·11	5·86	0	2	1·6	3	0	0·06	0·75	0	0	0	2·2	0·56	0	0	0·67
Nym	*Nymphea alba*	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Pha	*Phalaris arundinacea*	0·44	2·43	0	0	0·5	2·3	1·89	1·53	2·88	4·89	4·32	0	0	0·11	1·85	1·88	2
Phl	*Phleum arvense*	0	0	0	0	0	0	0	0	0	0	0·5	0	0	0	0	0	0
Phr	*Phragmites australis*	1·33	3·14	0·8	0·23	5·9	0·6	2·11	2·53	2	0	0	0	4·6	1·56	0	0	0
Pla	*Plantago major*	0	0	0	0	0	0	0	0	0	0·33	0·23	0	0	0	0	0	0
Phy	*Polygonum hydropiper*	0·22	1·71	0	0	0	0·1	0	0	0	0	0·73	0	0	0	0·15	0	0
Pop	*Populus nigra*	0	0	0	0	0	0	0·22	0	0	0	0·09	0	0	0	0	0	0
Pco	*Potamogeton coloratus*	0	0	1·4	0	0	0	0	0	0	0	0	3·11	0	0·89	0	0	0
Pcr	*Potamogeton crispus*	0	0·14	0	0	0	0	0	0	1·25	0	0	0	0·4	0	0	0	0
Plu	*Potamogeton lucens*	0	0	0	0	0	2·2	0	0	0	0	0	0	0	0	0	0	0
Pna	*Potamogeton natans*	0	0·43	0·5	0	0·4	1·2	0	0·71	0·5	0	0	1·22	1	2	0	0·63	2·5
Pno	*Potamogeton nodosus*	0	0	0	0	0	0	0	0	0	0	0·23	0	0	0	0	0	0
Ppe	*Potamogeton pectinatus*	0	1·86	0	0·08	0	1·2	0	0·12	4·38	0	0·09	0	0	0	0	0	0
Ppf	*Potamogeton perfoliatus*	0	0	0	0	0	0·8	0	0	0	0	0·05	0	0	0	0·92	0·5	0·17
Ppu	*Potamogeton pusillus*	0	1·29	0	0	0	0·8	0	0	0	0	0·55	0·78	0·6	0	1·15	1·38	0·33
Pot	*Potentilla reptans*	0	0	0	0	0	0	0	0	0	0·56	0	0	0	0	0	0	0
Pru	*Prunella vulgaris*	0	0	0	0	0	0	0·11	0·24	0	0·33	0	0	0	0	0	0	0
Rci	*Ranunculus circinatus*	0·89	1·14	0	0·23	0	1·5	0	0	2·13	0	0·91	0	0	0	0·23	1·75	0

Table 2—contd

Rfl	Ranunculus flammula	0	0	0	0	0	0	0·67	0	0	0	0	0	0	0	0	0	0
Rre	Ranunculus repens	0	0	0	0	0	0	0·44	0·06	0	0·56	0·27	0	0	0	0	0	0
Rtr	Ranunculus trichophyllus	0·11	0·14	0	0	0	0	0	0·12	0·38	0	0·09	0	0·2	0	0	0	0
Ror	Roripa amphibia	0·44	2·43	0	0	0	0·90	0	0·94	3·38	0·44	1	0	4	0	0·08	0	1
Rub	Rubus sp.	0	0	0	0	0	0	0·11	0·18	0	0·56	0·36	0	0	0	0	0	0
Rum	Rumex hydrolapathum	0	0	0	0	0	0	0	0	0	0·22	0	0	0	0	0	0	0
Sag	Sagittaria sagittifolia	0	0·86	0	0	0	2·0	0	0	0	0	0	0	0	0	0	0·75	0
Sci	Salix cinerea	0	0	0·3	0	0	0	0	0·47	0	0	0	0	0	0	0	0	0
Sal	Salix sp.	1·11	0·43	1·2	0	0	0·4	0·11	1·88	0·25	1·33	0·45	0	1·2	0	0	0	0
Sam	Sambucus edulus	0	0	0	0	0	0	0	0	0	0	0·14	0	0	0	0	0	0
Sla	Scirpus lacustris	0	0·71	0·1	0·31	0·3	0·6	0	0·12	1·63	0·78	0·09	0	0·2	0·22	0·08	0·25	0·5
Sen	Senecio aquaticus	0	0	0	0	0	0	0	0	0	0·22	0·09	0	0	0	0	0	0
Sgi	Solidago gigantea	0·56	0	0	0	0	0	1·89	0·41	0	0·89	0·18	0	0	0	0	0	0
Sem	Sparganium emersum	0	3·71	0	0·15	0·3	2·6	0	0·29	1·75	0·78	0·32	0·22	0·8	1·22	1·62	2·75	2·5
Ser	Sparganium erectum	0	0	0	0	0·3	0	0	0	0	0	0	0	1·2	0	0	0	0
Sta	Stachys palustris	0	0	0	0	0	0	0	0	0	0	0·23	0	0	0	0	0	0
Sym	Symphytum officinale	0	0	0·3	0	0	0	0·78	0	0	0	0	0	0	0	0	0	0
Tan	Tanacetum corymbosum	0	0	0	0	0	0	0	0	0	0	0·09	0	0	0	0	0	0
Tar	Taraxacum sp.	0	0	0	0	0	0	0	0	0	0·22	0·09	0	0	0	0	0	0
Typ	Typha latifolia	0	0	0	0	0	0	0·22	0·06	0	0	0	0·11	0	0	0	0	0
Umi	Utricularia minor	0	0	0	1	0·1	0	0	0	0	0	0	0	0	0	0	0	0
Vbe	Veronica beccabunga	0	0·43	0	0·08	0	0	0	0·29	0·5	0	0·45	0	0	0	0	0·25	0
Zan	Zannichellia palustris	0	0	0	0	0	0·1	0	1·59	0	0	0	0	0·2	0	0	0	0·33

by the hill-side aquifer from the left side of the flood-plain, characterized mainly by high nitrate content and conductivity. The other six channels (BIL2, MAL, MAR, MIL3, BIR1 and BIR2) all have positive values on the F1 axis, related to low values of conductivity, alkalinity, and phosphate, nitrate and silica contents. Meanders (M-channels) were distributed everywhere on the figure, whereas all the braided channels are grouped with positive values on the F2 axis. Aggraded meanders (MAL and MAR) are quite close on the factorial map, despite their location on different sides of the river, and could be supplied by river seepage, characterized by low values of conductivity and nitrate content (Table 1).

The channels located along the right side of the river (MAR, BIR1 and BIR2) are also relatively close on the factorial map, even though they have different geomorphological origins and incision levels (aggraded meander for MAR vs incised braided channels for BIR1 and BIR2). They could be all supplied by seepage but BIR1 and BIR2 could also be supplied by the aquifer from the right side of the floodplain as they are located in an incised reach. In this case, the aquifer does not have high nitrate content or high conductivity (Table 1), and is not distinguishable from river seepage among the variables studied.

The Ain River site was the only site that had positive values on the F1 axis and negative values on the F2 axis reflecting its high pH and oxygen content and low values of the other variables. Despite its location in the floodplain, MIL3 is far from MIL1 and MIL2 on the
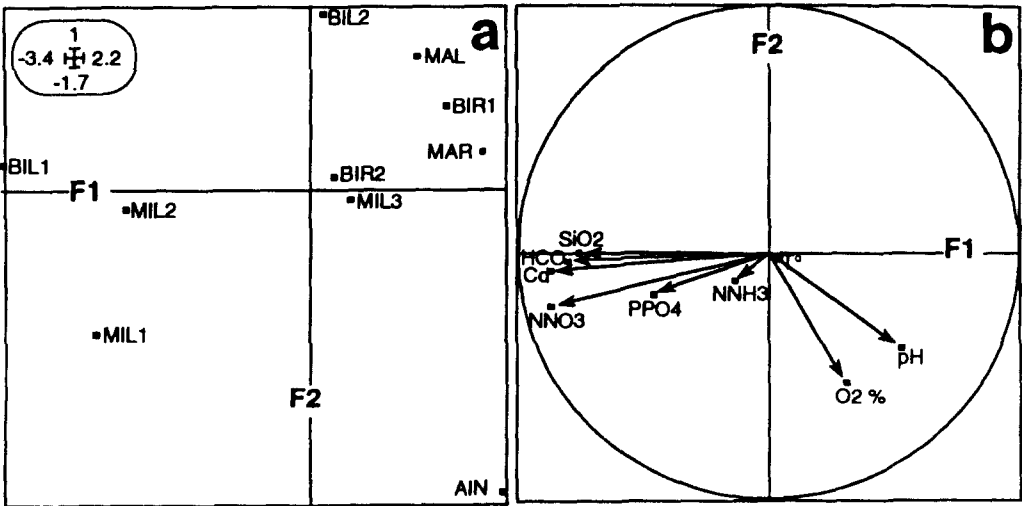

Fig. 3. Between-class normalized PCA of the physico-chemical data; (a) F1×F2 factorial map of the channels; (b) correlation circle of the chemical variables with the two first axes of the analysis. See Fig. 1 for codes and Fig. 2 for location of the sampling stations.

factorial map, suggesting that it is not (or only slightly) supplied by the left side aquifer.

4.2. Floristic communities

4.2.1. Cut-off channels

The cPCA on the whole plant dataset illustrates the mean floristic differences between the channels, without considering any heterogeneity of communities within the channels (Fig. 4). The first two axes contributed 27 and 24% of the total variation, respectively. Incised meanders located along the left side of the river are dissociated on the factorial map, as MIL3 and MIL1 have negative values on the F1 axis and positive values on the F2 axis, whereas MIL2 is located on the negative side of the F2 axis (Fig. 4(a)). MIL3 and MIL1 are characterized mostly by *Nuphar lutea* and *Myriophyllum verticillatum*, and, for a minor part, *Ceratophyllum demersum* and *Phragmites australis* (Fig. 4(b); Table 2).

MIL2 is located close to (1) the braided incised channels located on the left side of Fig. 4(a) (BIL1 and BIL2); (2) one of the incised braided channels located on the right side (BIR2), and (3) the aggraded meander located on the left side (MAL). This group of stations contained *Carex elata*, *Juncus articulatus*, *Mentha aquatica*, *Chara major*, and for a minor part, *Potamogeton coloratus*, *P. natans*, *Cladium mariscus*, and *Berula erecta*.

Finally, MAR and BIR1 form a distinctive third group related to the presence of *Phalaris arundinacea*.

The hypothetical groups proposed in Fig. 1 can be superimposed on the factorial map of the cut-off channels. The incised meanders (MIL1, MIL2, and MIL3) were only partly grouped on the factorial maps, MIL2 being closer to incised braided channels (BIL1, BIL2,

BIR2). The analysis did not separate the left from the right side of the river among these channels, and only BIR1 was distinguished from the others. Aggraded meanders (MAL, MAR) were separated from the other channels on the factorial map, but differed floristically from each other. MAR and BIR, both located along the right side of the river, were close together on the factorial map, whereas BIR2 appeared close to the channels having the same geomorphological origin, but located along the left side.

4.2.2. Floristic zones

Within each cut-off channel, the simple cPCA separated out individual sampling plots along three significant axes. Thus, the 43 plots in MAL were grouped into four floristic zones MAL_{1-4}, the 33 plots in MIL into three zones MIL_{1-3}, and BIL1, MIL1 and BIR1 into two zones each, zone 1 always referring to the upstream end of the cut-off channel. The other four sites (MIL2, BIL2, BIR2 and MAR) were considered as homogeneous by the analysis and were consequently not divided into floristic zones.

The first four axes of the between-class cPCA of the zone dataset were found to account for 66% of the total variation (22.8, 18.1, 14 and 11%, respectively), so, both the F1×F2 and F3×F4 factorial maps were considered. The different zones of the channels were clearly separated on the F1×F2 factorial map (Fig. 5(a)), indicating the high heterogeneity of their macrophyte communities. No clear group of zones was exhibited, as most of the zones were ranged along a double gradient, from negative values on F2 axis (and both negative and positive values on F1 axis) to positive values on the same axis. Negative values on both F1 and F2 axes corresponded to the downstream parts of the incised
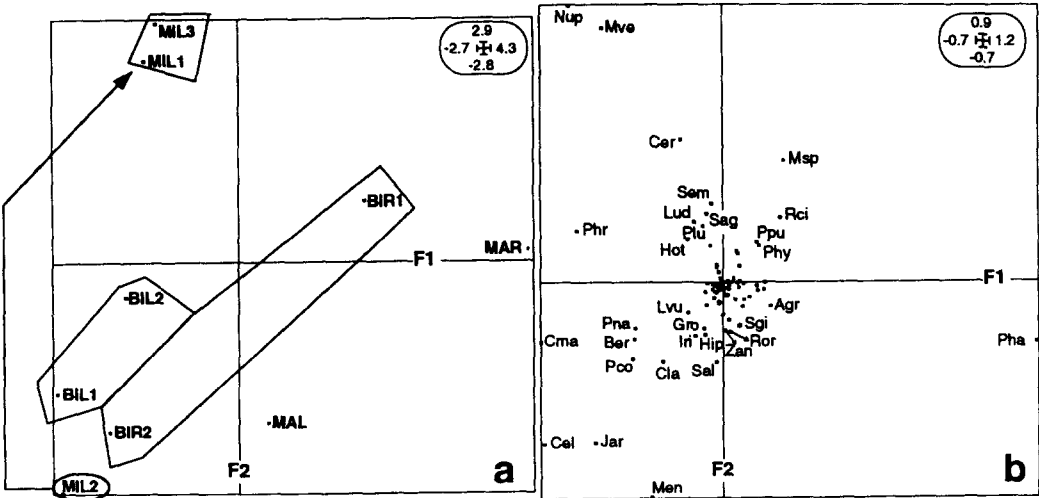

Fig. 4. Between-class cPCA (channels as classes) of the floristic data set; (a) F1×F2 factorial map of the channels with polygons indicating the hypothetical groups of the Fig. 1; (b) F1×F2 factorial map of the species (for species abbreviations, see Table 2). See Fig. 1 for codes and Fig. 2 for location of the sampling stations. Abbreviations of species close to the origin of the axes are not shown.

meanders MIL3$_3$ and MIL1$_2$, and to a downstream zone of the aggraded meander MAL$_3$. These zones were related to *Nuphar lutea*, but also to meso-eutraphent species such as *Elodea canadensis, Sparganium emersum, Potamogeton pectinatus, Callitriche platycarpa* and *Rorippa amphibia* (Kohler et al., 1974; Wiegleb, 1978; Castella and Amoros, 1986; Klein and Carbiener, 1989; Bornette et al., 1996a) (Fig. 5(b)).

The incised braided channels BIL1$_2$, BIR2, BIL2, and the medium zones of the incised meander MIL3$_2$ and of the aggraded meander MAL$_2$ all lay close together with positive values on the F1 axis and negative values on the F2 axis (mostly for BIL1$_2$), characterized by *Phragmites australis* and *Berula erecta* for negative values on F2 axis, and *Chara major, Carex elata, Juncus articulatus, Mentha aquatica* for positive values on F1 axis. The incised braided channel BIR1 and the aggraded meander MAR are located on negative values on F1 axis and more or less positive values on F2 axis. These floristic

zones were characterized by the presence of *Phalaris arundinacea* and *Myriophyllum spicatum* combined with the absence of *Phragmites australis*. When the zones are grouped according to the hypothetical typology of Fig. 1 into meanders vs braided channels, incision vs agradation, or left vs right sides, Fig. 5 again shows no clear discrimination on the basis of plant communities. Only two of the three channels located of the right side (MAR, BIR1, BIR2) were grouped by the analysis.

The F3×F4 factorial map of the analysis focused more on the differences between channels (Fig. 6 (a)). The braided channels (BIL1 and 2, BIR1 and 2) are not placed close to the meanders on the factorial map as they are grouped on the negative side of the F4 axis.
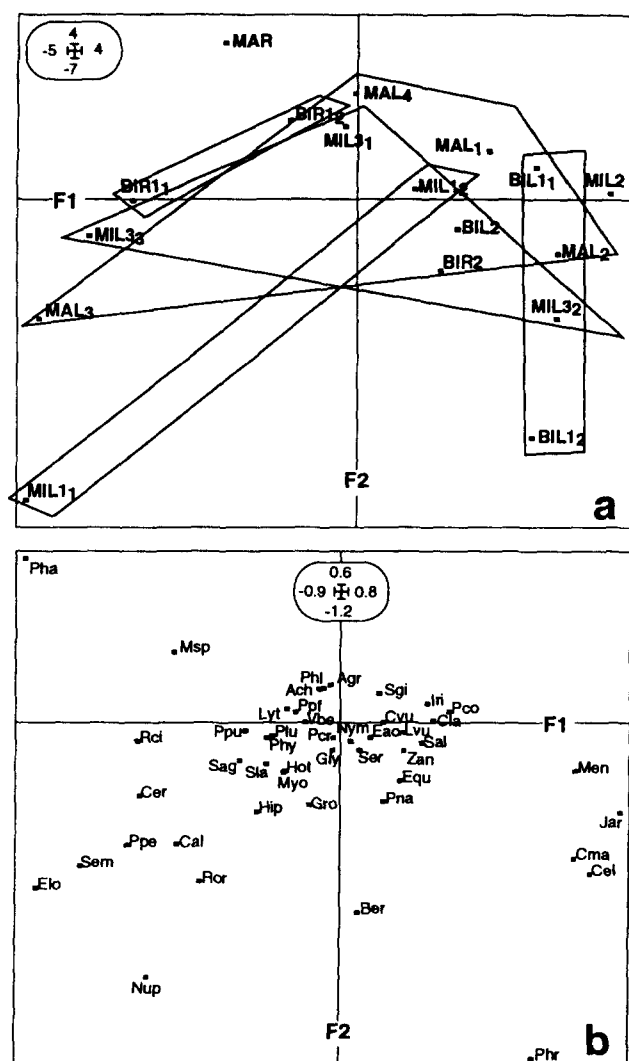
Fig. 5. Between-class cPCA (floristic zones as classes) of the floristic data set; (a) F1×F2 factorial map of the channels; (b) F1×F2 factorial map of the species (other details as in Fig. 4).
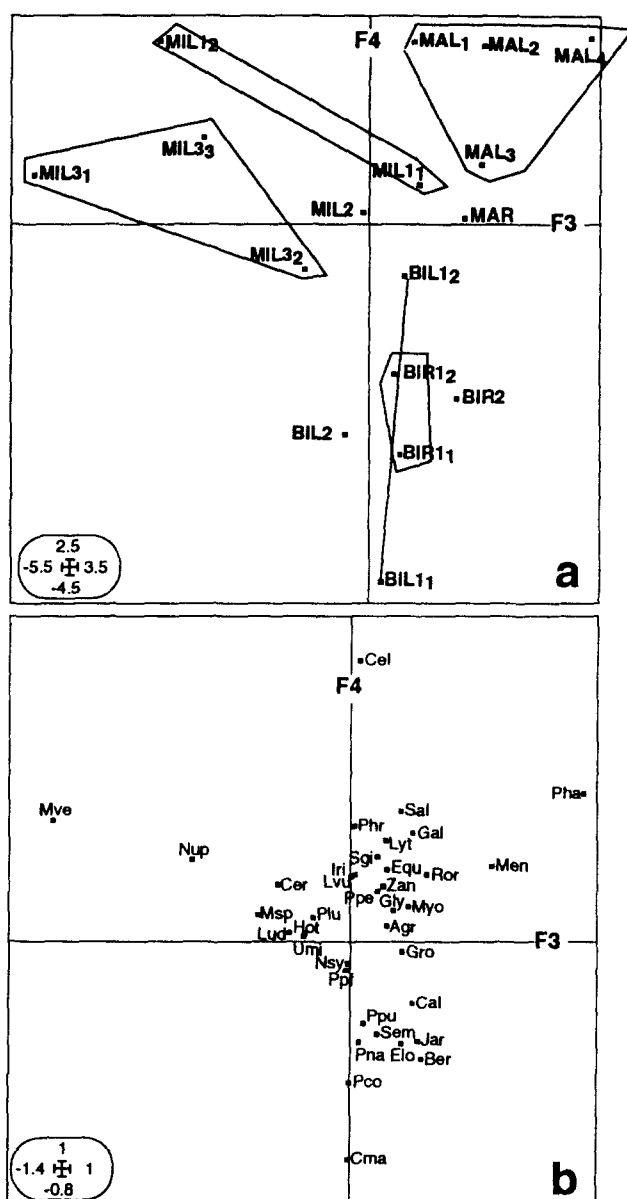
Fig. 6. Between-class cPCA (floristic zones as classes) of the floristic data set; (a) F3×F4 factorial map of the channels; (b) F3×F4 factorial map of the species (other details as in Fig. 4).

They were characterised by the oligotraphent species *Chara major*, *Potamogeton coloratus*, *P. natans*, *Berula erecta* (associated with *Mentha aquatica*), *Juncus articulatus* (Kohler et al., 1974; Wiegleb, 1978; Kohler and Schiele, 1985; Carbiener et al., 1990), and the species of more eutrophic and flood disturbed ecosystems *Elodea canadensis*, *Sparganium emersum*, *Potamogeton pusillus* and *Callitriche platycarpa* (Bornette and Amoros, 1991; Bornette and Large, 1995).

The aggraded cut-off channels (MAL and MAR) are grouped and have positive scores on the F3 and F4 axes owing to the abundance in these channels of *Phalaris arundinacea*, *Mentha aquatica*, and/or *Carex elata* (Fig. 6(b)).

5. Discussion

Channels ranged along a gradient of nutrient content of the water. This gradient is due to (1) seepage supplies from the river which is richer in nutrients, and (2) the occurrence of aquifers poorer in nutrients.

5.1. Cut-off meander channels

Species of calm, undisturbed waters, as *Nuphar lutea*, *Carex elata*, or *Phragmites australis* were usually associated with cut-off meanders (Cernohous and Husak, 1986; Balocco-Castella, 1988; Bornette et al., 1994a). *Myriophyllum verticillatum*, considered as a mesotraphent species, and *Ceratophyllum demersum*, considered as an eutraphent species, were also usually associated to these channels (as determined by [PO_4^{2-}] and [NH_4^+] contents of the water (Kohler et al., 1974; Haslam et al., 1975; Kohler, 1975; Cernohous and Husak, 1986; Klein and Carbiener, 1988; Bornette et al., 1996a).

Callitriche platycarpa, *Potamogeton pusillus*, *Sparganium emersum*, *Elodea canadensis*, *Berula erecta*, and *Potamogeton natans*, considered as flood-tolerant species (Bornette and Amoros, 1991; Bornette and Large, 1995), were usually found together and were more abundant in braided channels.

Phalaris arundinacea is found on frequently moved sandy substrates (Pautou, 1975; Petit and Schumacker, 1985; Castella and Amoros, 1986), and indicates usually a strong influence of flood disturbances. This species, together with *Mentha aquatica*, which is favoured by groundwater supplies (Bornette and Large, 1995; Bornette et al., 1996a) occurred in the two aggraded meanders MAL and MAR. These two meanders were separated from the other meanders in Figs. 4 and 6, which indicates that they were more frequently overflowed. MAL and MAR were also similar through their water characteristics (Fig. 3), as a result of their aggraded situation that favored seepage from the river.

Carex elata grows in channels undisturbed by floods or in protected areas along banks in the disturbed ones (Pautou and Girel, 1986; Castella and Amoros, 1986). This species, together with *Nuphar lutea*, *Phragmites australis*, *Myriophyllum verticillatum*, and *Ceratophyllum demersum* was associated with MIL1 and MIL3, two incised meanders grouped through the floristic data analyses (Figs. 4 and 6). The analyses of chemical data gave apparently opposite results, as MIL3 was similar to MIL1 through its floristic communities, but dissimilar in its chemistry. Despite its location, MIL3 seemed not to be influenced by the left hill-side aquifer. The location of the channel, further from the hillslope than MIL1, could be an explanation. A local geological difference (occurrence of clay) could have impeded the drainage of the aquifer into the cut-off channel.

Chemical data indicated that MIL2, like MIL1, was mostly supplied by water from the left side aquifer. *Chara major*, *Potamogeton coloratus*, *Cladium mariscus*, *Mentha aquatica*, and *Berula erecta* occurred only in MIL2. These species are considered as oligotraphent species (Kohler and Schiele, 1985; Carbiener et al., 1990; Rodwell et al., 1995). The shallowness of MIL2 (≤ 1 m deep at the date of floristic sampling) compared to MIL1 ($0 \cdot 9$–3 m deep) probably increased the rate of water change from the aquifer.

5.2. Cut-off braided channels

Cut-off braided channels (BIL1, BIL2, BIR2, BIR1) supported a group of flood-tolerant species, such as *Callitriche platycarpa*, *Potamogeton pusillus*, *P. natans*, *Sparganium emersum*, *Elodea canadensis*, and *Berula erecta*. However, some differences occurred between them. BIL1 and BIL2, located along the left side of the river, were clearly associated with oligotraphent species (*Chara major*, *Potamogeton coloratus*) but differed through physico-chemical characteristics. Only BIL1 was supplied mainly by the hill-side aquifer, while BIL2 was probably also influenced by river seepage (Fig. 3). This suggests that incision of the river was not sufficient to disconnect the river and BIL2 completely, and that seepage still supplied the channel.

BIR1 and BIR2, both located along the right side of the river, had very similar chemical characteristics. However, BIR1 appeared more like the aggraded meanders in its floristic composition (Figs. 4 and 5) and BIR2, in contrast, appeared closer to BIL1 and BIL2. Although it was located in an incised reach of the river, BIR1 seemed strongly influenced by river seepage and overflows. An explanation could be provided through the knowledge of the natural dynamics of the river. As a consequence of the process of river incision that has occurred throughout the 20th century, Bravard, 1986 and Marston et al. 1995 have demonstrated that the

channels that have been cut-off from the river more recently are closer in water levels to that of the river. Because BIR1 was cut-off very recently (between 1965 and 1973), its level is closer to the river level than the other, older, braided channels (BIR2 and BIL2 cut-off between 1871 and 1945, and BIL1 between 1871 and 1933).

The left side-hill aquifer mostly supplied the channels that were located close to the hillslope in the upstream part of the river under study (BIL1, MIL1, MIL2), whereas MAL3, located downstream, was less influenced. The location of the channel (along the hillslope or close to the river) therefore seemed to be another feature that could determine its chemical characteristics.

5.3. Comparison of hypothetical typology with observations

The analyses of floristic and chemical data sets demonstrated the structuring effect of the processes involved in Fig. 1. However, because numerous processes interact, each analysis only partly verified the hypothetical typology of the figure, and the two components (vegetation and physico-chemistry) afforded complementary information on wetland characteristics. The results demonstrated that the proposed typology was not sufficient to explain the functioning of each of the channels, and that some other features, such as the age of the channel, its depth, or its location in the floodplain (close or far from the hillslope vs the river) should also be considered.

Thus, the complexity observed at the landscape scale results from the fluvial dynamics (geomorphological pattern and incision), and from the nutrient content of the water, induced by the origin of the water supplies. This complexity is also increased by the fact that the time scale of some geomorphological processes (creation of braided or meandering landforms during the 19th and 20th centuries) interacts with the time scale of biological processes (mainly ecological succession) which are partly determined by incision of the river in the past 20 years. As a consequence, in a small floodplain section (15 km long) some ecosystems frequently disturbed by floods (aggraded meanders, or some braided channels), occur together with some occasionally disturbed (some braided channels), and others, like incised meanders, rarely or never disturbed, each kind being characterized by particular assemblages of aquatic plants. In combination, eutraphent communities (in aggraded channels, supplied by river seepage) co-occur with oligotraphent ones (in incised channels, supplied by oligotrophic side-hill aquifer), and some intermediate cases also occur. A trophic gradient can also be observed within the longest channels (meanders), if groundwater supplies, which dominate in the upstream part, faces river backflows in the downstream zone. Each ecosystem is a particular

case, resulting from a particular combination of ecological factors. However, the co-occurrence of numerous particular ecosystems results in a high biodiversity at the river landscape scale.

Floods are usually considered as disturbing events, destroying communities and resetting ecological successions. This study demonstrates the positive role of floods for increasing the biodiversity of communities at the floodplain scale. Indeed, such a floodplain supports species that are frequently observed in aquatic ecosystems, such as *Nuphar lutea*, and *Phragmites australis*. These species become dominant along floodplains, as a consequence of eutrophication and river regulation decreasing overflowing frequency (Tomaszewicz, 1969; Brock et al., 1987; Rath, 1987; Bornette et al., 1994a). However, more rare flood-tolerant and mesotraphent to oligotraphent species also occur in the studied section, e.g. *Potamogeton natans*, *P. coloratus*, *Alisma ranunculoides*, *Groenlandia densa*, and *Chara major*, which indicate some fluvial dynamics in the studied channels.

The decrease in flood frequency and lateral erosion results in the decrease, and even the complete cessation, in creation of new fluvial landforms. Natural succession processes then lead to the disappearance of those wetland communities that are adapted to flood disturbances, whereas plant diversity and the maintenance of rare species are favoured in cut-off channels where flood disturbances still occur (Bornette and Large, 1995; Bornette and Amoros, 1996a). At the floodplain scale, this implies the maintenance or the restoration of the possibilities for migration of the river bed in the most favorable sectors. Such conservation measures should take into account all the processes that interact on several time-scales. They should also consider all the ecosystems of the river floodplain, as each ecosystem is involved in the biodiversity at this scale.

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