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A comparitive study of the hydrophyte flora from the Alpine Rhine to the Middle Rhine. Application to the conservation of the Upper Rhine aquatic ecosystems

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Abstract

A typology of the main channel of the river Rhine according to its aquatic bryophyte and vascular hydrophyte assemblages is presented. The aquatic bryophytes are especially abundant in the main channel, having found stable, rocky habitats with variable water levels in the regulated river, and segregate longitudinally along a gradient of water quality. Conversely, the vascular hydrophytes are restricted to side channels with constant discharges and silt deposits, and segregate laterally along a gradient of connectivity with the main river. The hydrophytes have been affected by water eutrophication which became obvious in the 1960s–1970s. The oligotrophic groundwater-fed side-channels disconnected since the river canalization consequently include a relic reference flora. Important hydraulic works are currently in progress in order to protect the areas located downstream from the canalized Rhine from flooding by retaining the river waters in lateral systems during the discharge peaks and to recreate a functional alluvial floodplain by reconnecting the disconnected side-channels to the main river. The floodpulse caused by the suddent input of surface water in the disconnected brooks will probably wash out most of the hydrophytes and it is very likely that the rare species with their low recolonization strategies will disappear in these conditions. It is highly desirable to preserve from flooding the last oligotrophic brooks with their original hydrophyte assemblages. Those brooks which show a tendency to silt up can be redynamized by ecological engineering without disturbing the flowing drains of the watertable. In areas (including flowing drains of the watertable) that have already been designated for flood retention, the hydraulic works should allow, as far as possible, the preservation of the flowing oligotrophic streams by only permitting the input of surface water in the silted-up brooks. The disconnected side-channels could then continue their role as refugia from where the main channel, whose water quality has been improving for a decade, could be recolonized by its primary flora.

Keywords: Rhine; Regulation; Zonation; Floods; Refugia

1. Introduction

The classification of running waters is based on topography (system of Illies & Botosaneanu), the fall of the river (system of Illies) or on the main fish species occurring from the springs to the estuary (system of Huet) (Jeuniaux, 1990). All of these systems are on a par with upstream–downstream patterns of oxygen concentration, temperature, granulometry of the alluvium and physico-chemical composition of the water. Community structure and niche relationships of stream bryophytes (Glime, 1970; Vitt et al., 1986; Glime and Vitt, 1987; Muotka and Virtanen, 1995) and vascular hydrophytes (Karpati, 1963; Haslam, 1982; Kohler, 1982; Wiegleb, 1984; Kohler and Schiele, 1985; Carbiener et al., 1990) also depend on these factors and are correlated with specific structural adaptations (Vitt and Glime, 1984). However, bryophyte zonations at basin scale are few documented (Glime, 1970). Several regional studies have already been conducted in the large European rivers. The hydrophytes of the Rhine were studied in Lake Constance (Lauterborn, 1941; Lang, 1968; Ahrens, 1992), in the High Rhine (Lauterborn, 1916; Jaag, 1938; Philippi, 1961, 1968), in the Upper Rhine (Lauterborn, 1910; Philippi, 1968; Krause, 1981a; Schütz, 1993; Vanderpoorten et al., 1998) and in the Lower Rhine (Frahm and Abst, 1993) but no synthesis at basin scale has yet been performed. In this paper, a

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study of the changes in the hydrophyte assemblages from the Alpine Rhine to the Middle Rhine along about 1000 km is presented. The typology of the Rhine flow based on hydrophyte assemblages enables the evaluation of the degree of similarity between the study sites so as to answer the following questions: what are the main ecological factors responsible for the hydrophyte zonation, to what extent has the regulation of the river modified this zonation and which management practices should be proposed for conserving the most interesting hydrophyte assemblages?

2. Study area

The Rhine was studied for about 1000 km from its sources in Switzerland to Köln in Germany (Fig. 1), and was divided into five hydrogeomorphological sectors (Fig. 2). The main physico-chemical factors measured at the stations of the International Commission for the Preservation of the Rhine against Pollution and of the Gernan Commission for Water Quality of the Rhine are given in Fig. 2.

The features of these sectors have progressively been modified by the regulation of the river. In the High Rhine, almost all the former rapids disappeared following the construction of hydroelectric powerstations which caused the water level to increase upstream from the barrages. In the Upper Rhine, which flows in an alluvial floodplain a few kilometres wide and is characterized by numerous side-channels and mobile pebbly alluvium banks disturbed each year by floods, the modification of the river began in the 19th century in order to provide protection from flooding. The continual moving of the gravel and sandbanks, even after the rectification measures, as well as the low water depth in period of low discharges, were seen as an unacceptable disadvantage for navigation. The Upper Rhine regulation was therefore started at the beginning of the 20th century. A low water channel with a width of only 80 m was maintained by the construction of groins in the river bed (Dister et al., 1990). This caused an increase in the vertical erosive power of the river. Between 1870 and 1950, the water level was lowered by 5–7 m in the areas downstream from Basel, and rapids progressively emerged at the level of the village of Istein. Consequently, the Upper Rhine was canalized between France and Germany to allow navigation between Basel and Strasbourg as well as to produce hydroelectricity, so that most of the former side-channels were disconnected from the main river. Being almost exclusively fed by groundwater since the canalization, their discharge, which is currently of about 100 l/s, has become very constant. Some of the channels have a tendency to silt up.

The regulation of the river also led to the loss of about 100000 ha of functional floodplain between Basel and Bingen (Mock et al., 1991), which exacerbated the flood problems downstream from the canalized sector (Engel, 1996). Important hydraulic works are therefore currently in progress in the Upper Rhine in order to protect the areas located downstream from flooding. The aim of these works is to eliminate the exceptionally high discharge peaks of the Rhine by retaining the river waters in lateral systems locally called "polders". Because the Rhine valley includes important alluvial ecosystems at a European scale (Journal officiel des Communautés Européennes, 1992), the works also propose to re-activate the alluvial ecosystems disconnected since the river canalization by performing "ecological" flooding, for example:

1. by authorizing input discharges of Rhine water into the brooks when the discharge of the river is higher than 1550 m^3/s. Such discharges are reached on 50 days each year, according to a statistical study perfomed between 1978 and 1993 (Dillman, 1994). In the already functioning polder Altenheim (Germany), the input discharge has increased to 5 m^3/s per 100 m^3/s in the Rhine and up to 60 m^3/s when the Rhine discharge reaches 2500 m^3/s (Landesanstalt für Umweltschutz Baden-Württemberg, 1993);
2. by flooding the whole polder for 8–10 days when the discharge of the river is higher than 2000 m^3/s. These discharges are reached for mean 5 days in June and 4 in July (Dillman, 1994).

3. Methods

The hydrophytes were recorded separately (nomenclature of Corley et al., 1981; Corley and Crundwell, 1991 for the mosses; Grolle, 1983 for the liverworts; and Oberdorfer, 1994 for the vascular hydrophytes). If the definition of "hydrophyte" is clear for vascular plants, it is much less well defined for bryophytes. A definition such as that of Koppe (1945), who classified aquatic bryophytes as always growing in water or on the surface of it, is very restrictive, in so far as most of the stream bryophytes are present in the variable water level zone (Muotka and Virtanen, 1995). The outlines of the latter remain however poorly defined. Therefore, the data concerning the diversity of stream bryophytes vary greatly in the literature, making it difficult to give them an adequate ecological interpretation. In this paper, the typology of Düll (1992) was used to determine the bryophytes to be included in the analysis. Presence–absence was recorded in 95 10–30 m long samples for the aquatic bryophytes and in 30 samples for the vascular hydrophytes. The typology of the records according to their floristic composition was obtained by hierarchical aggregative numerical classification. Species

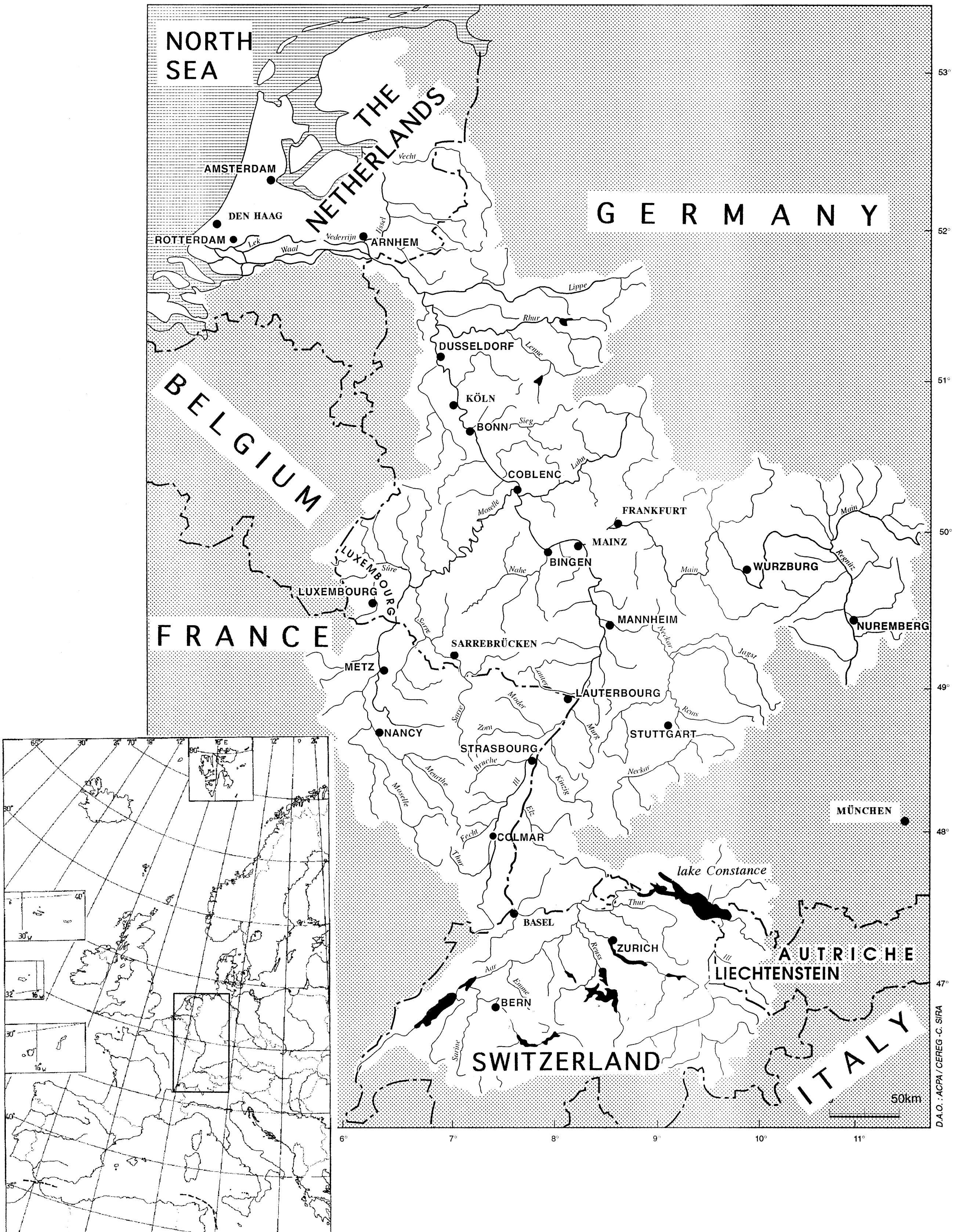
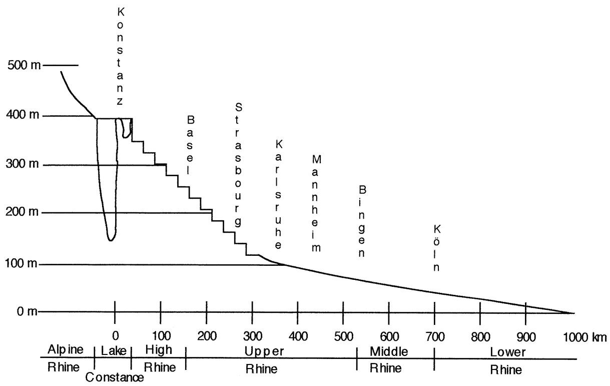


Fig. 1. The Rhine basin.



g	1	0.87	0.25	0.30
Q	1020	1220	1590	1976
m O2	11.5	11.0	9.75	9.50
min O2	8.5	5.0	5.0	6.50
m N-NH4+	0.10	0.15	0.50	0.40
max N-NH4+	0.25	0.50	1.75	1.25
m P-PO43-	0.10	0.10	0.35	0.20
max P-PO43-	0.15	0.25	1.00	0.40

Fig. 2. Longitudinal profile of the Rhine. g: average gradient (/1000); Q: average annual discharge (calculated from 1931 to 1980); m, max, min: annual mean, maxima and minima concentrations (mg/l) in 1987 (after Tittizer and Krebs, 1996).

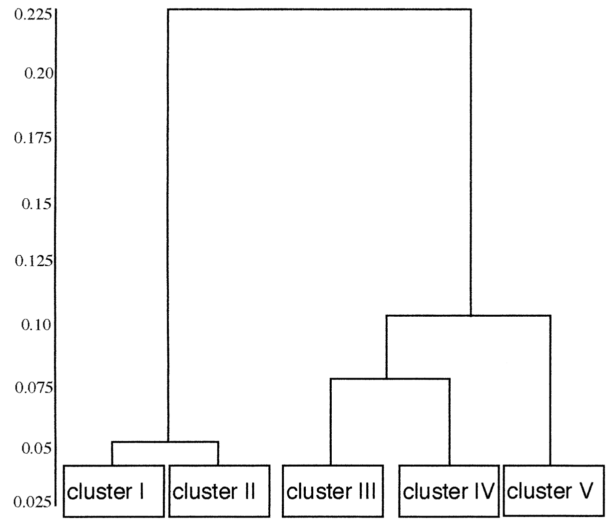


Fig. 3. Summary cluster diagram for the classification of the study sites according to their aquatic bryophyte assemblages using Ward's minimum variance criterion. Dissimilarity, indicated on the vertical axis, is the between clusters semi-partial *R*-squared.

occurring less than three times in the whole data set, which cannot be used to characterize a sector, were excluded from the analysis. Jaccard's coefficient c_j was used to measure the similarity between two records because it is well adaptated for nominal binary asymmetric variables (Kuo, 1996):

$$c_j = P/(P+N)$$

where P is the number of species in common between two records (co-presence) and N is the number of species present in one record but absent in the second.

The records were clustered from the Jaccard's distances matrix by using Ward's minimum variance criterion. The species fidelity to the clusters of records was measured by their relative conditional frequency in each cluster. This frequency is equal to the sum of the occurrences of the species i in the cluster of records j divided by the total number of records within the cluster j.

4. Results

Five clusters of records were retained after the procedure of classification according to the aquatic bryophyte assemblages (Fig. 3). The relative conditional frequencies of their characteristic species are given in Table 1. The first cluster (I) is characterized by mosses such as *Cinclidotus riparius*, *Octodiceras fontanum* and *Amblystegium riparium*. It includes records from the Upper Rhine downstream (including five records of Ahrens, 1995) and the Middle Rhine. The second cluster (II) is characterized by mosses such as *Cinclidotus danubicus* and *Rhynchostegium riparioides*. It includes records from the downstream part of the High Rhine and of the upstream part of the Upper Rhine. The third cluster (III) is characterized by mosses such as *Cratoneuron filicinum* and *Fissidens crassipes*. It includes records from Lake Constance (including five records of Ahrens, 1992), the upstream part of the High Rhine and disconnected Alsatian side arms. The fourth cluster (IV)

Table 1
Conditional relative frequencies of the characteristic aquatic and subaquatic bryophytes of the floristic clusters

	Cluster				
	I	II	III	IV	V
Octodiceras fontanum	0.64	0.00	0.00	0.00	0.00
Didymodon nicholsonii	0.48	0.00	0.00	0.00	0.00
Leskea polycarpa	0.61	0.28	0.00	0.00	0.00
Cinclidotus riparius	1.00	0.85	0.00	0.15	0.00
Amblystegium riparium	0.84	0.86	0.58	0.00	0.00
Cinclidotus danubicus	0.71	0.93	0.16	0.00	0.00
Amblystegium fluviatile	0.64	1.00	0.16	0.00	0.00
Fissidens crassipes	0.48	0.64	0.83	0.05	0.00
Rhynchostegium riparioides	0.09	0.78	0.41	0.05	0.00
Fontinalis antipyretica	0.09	0.71	0.35	0.25	0.00
Hygrohypnum luridum	0.06	0.14	0.25	0.75	0.00
Cratoneuron filicinum	0.09	0.42	0.83	0.80	0.00
Palustriella commutata	0.00	0.00	0.00	0.45	0.64
Philonotis fontana	0.00	0.00	0.00	0.45	0.64
Blindia acuta	0.00	0.00	0.00	0.1	0.57
Hygrohypnum smiths	0.00	0.00	0.00	0.05	0.21
Jungermannia exsertifolia	0.00	0.00	0.00	0.05	0.28
Philonotis seriata	0.00	0.00	0.00	0.05	0.78
Calliergon sarmentosum	0.00	0.00	0.00	0.00	0.21
Drepanocladus exannulatus	0.00	0.00	0.00	0.00	0.28
Dicranella palustris	0.00	0.00	0.00	0.00	0.71

Roman numbers related to clusters are those described in text.

is characterized by mosses such as *Hygrohypnum luridum*, *Cratoneuron filicinum* and *Palustriella commutata*. It includes records from the Alpine Rhine, the Anterior and Posterior Rhine and disconnected Alsatian side arms. The fifth cluster (V) is characterized by mosses such as *Philonotis seriata* and *Hygrohypnum smithii*. It includes records from alpine springs and rivulets at an altitude higher than 2000 m. The distribution of the aquatic bryophyte clusters in the study area is presented in Fig. 4.

Five clusters of records were also retained after the procedure of classification according to the vascular hydrophyte assemblages (Fig. 5). The relative conditional frequencies of their characteristic species are given in Table 2. The first cluster (I) is characterized by Lemnaceae, *Potamogeton pectinatus*, *Myriophyllum spicatum*, *Sparganium emersum* and *Elodea nuttallii*. It includes records from the Upper Rhine main channel and Upper Rhine side-channels still connected to the main river. The second cluster (II) is floristically different from I by the absence of *Lemna gibba* and the presence of *Potamogeton friesii*. It includes records from side channels with complex feeding, being almost exclusively fed by groundwater during low discharges in the Rhine and by surface water from the main river during the high discharges of the latter. The third cluster (III) is characterized by the mixing of the characteristic assemblage of cluster II with species such as *Groenlandia densa*, *Elodea canadensis*, *Berula erecta*, *Lemna trisulca* and *Callitriche obtusangula*. It includes records from downstream disconnected side-channels mainly fed by groundwater. The fourth cluster (IV) is floristically differentiated from cluster III by the absence of the characteristic assemblage of cluster II. It includes records from upstream disconnected side-channels exclusively fed by groundwater. The fifth cluster (V) is characterized by the only *Potamogeton crispus* and *Callitriche obtusangula*. It includes records from springs draining the watertable along the canalized Rhine. The distribution of the vascular hydrophyte clusters in the studied area is presented in Fig. 4.

5. Discussion

5.1. Assessment of the ecological factors causing the floristic zonation

The main channel of the river Rhine is characterized by rocky or pebbly substratum and variable discharges.

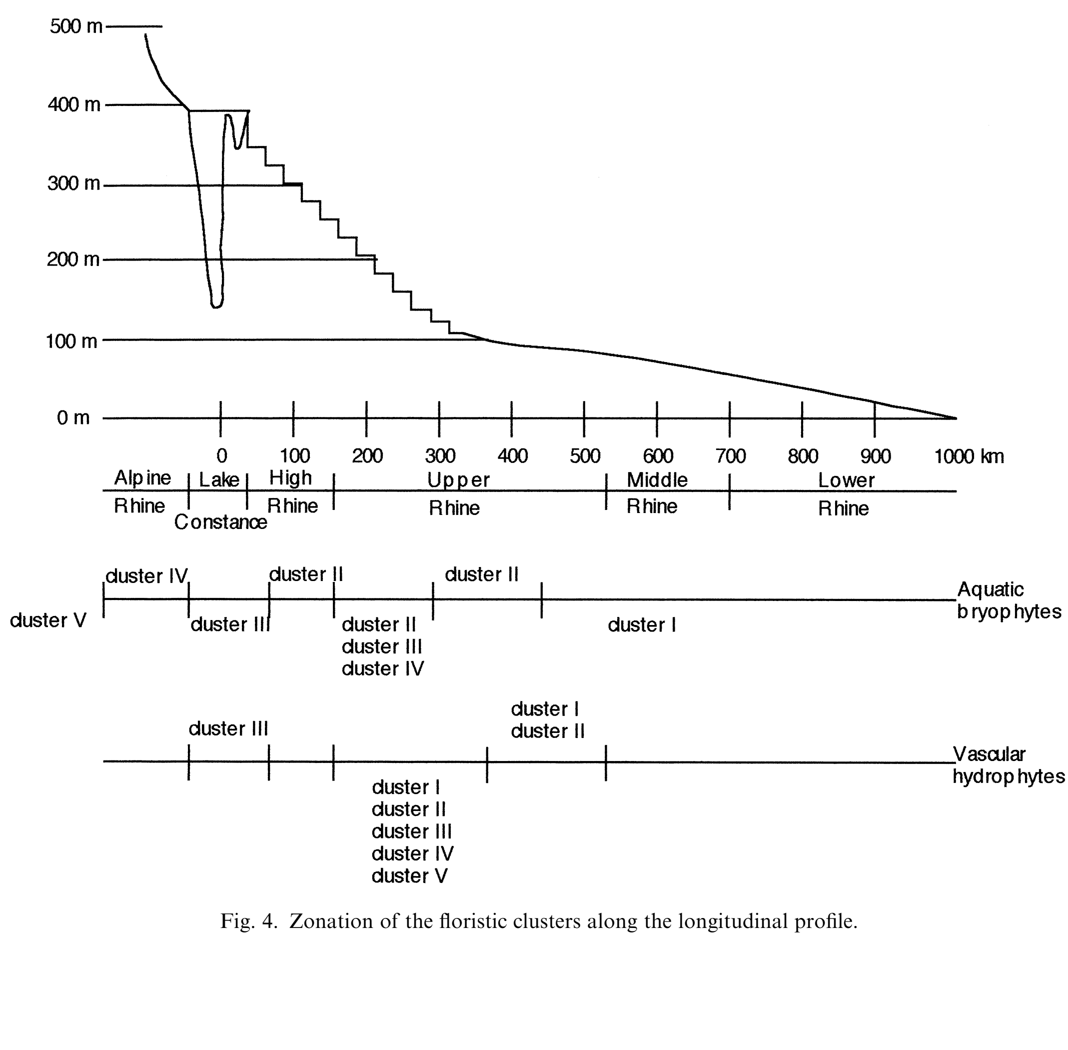


Fig. 4. Zonation of the floristic clusters along the longitudinal profile.

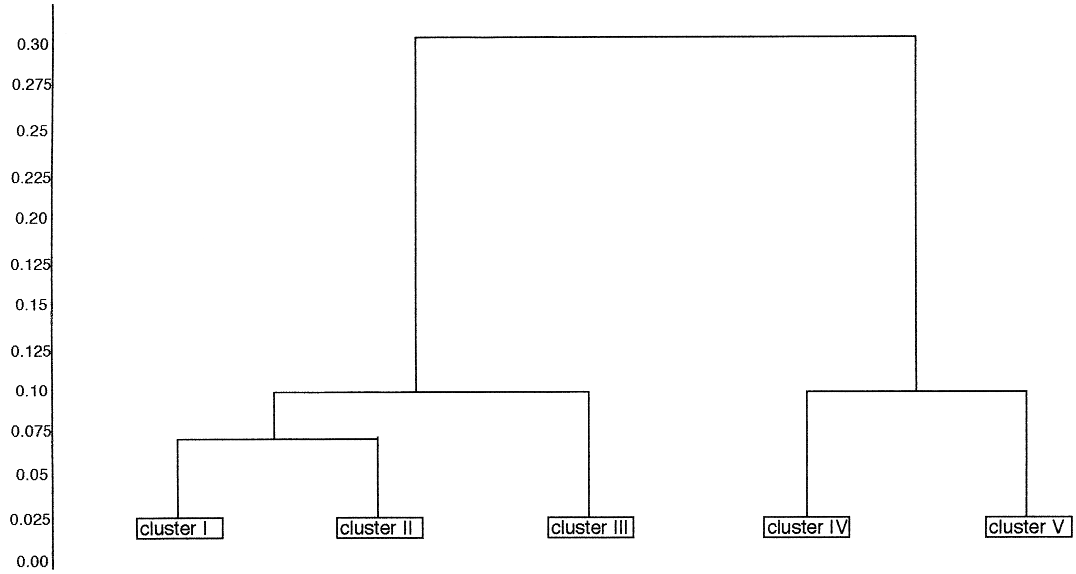


Fig. 5. Summary cluster diagram for the classification of the study sites according to their vascular hydrophyte assemblages using Ward's minimum variance criterion. Dissimilarity, indicated on the vertical axis, is the between clusters semi-partial R-squared.

These are two main factors unfavourable to the vascular hydrophytes (Preston, 1995), so that the main channel of the river has always been almost free of aquatic phanerogams. Conversely, the river banks have always exhibited a rich aquatic bryophyte flora (Lauterborn, 1910, 1916). The bryophyte typology, as opposed to the vascular hydrophyte typology, consequently shows a continuous zonation of assemblages. The bryophyte typology differs from the hydrogeomorphological classification downstream from Lake Constance, because the regulation of the river led to the homogenization of the habitat conditions. This has greatly influenced the composition of the hydrophyte communities. At the beginning of the 19th century, the High Rhine was characterized by a succession of rapids and waterfalls. These were natural places for rheophilous mosses presenting structural adaptations to the strength of the flow; for example, strong rhizoïds (*Rhynchostegium riparioides*), keeled leaves (*Fontinalis*), multicellular leaf margin (*Cinclidotus*) (Vitt and Glime, 1984). Downstream from Basel, the Upper Rhine lies in a much broader alluvial floodplain. The bed of the river was consequently composed of pebbly strands. Substrate movements under high flow can open up places which allow less competitive species to establish (Vitt et al., 1986; Muotka and Virtanen, 1995). This was, for example, the case for the pioneer Characeae in the young water-courses freshly excavated (Krause, 1969). Conversely, these sandy or pebbly strands, being disturbed every year, were obviously not favourable for the bryophyte flora. In the Middle Rhine, in the area of St Goar, only four aquatic bryophyte species were known: *Cinclidotus fontinaloides* and *Amblystegium riparium* that were common, *Hygrohypnum luridum* and *Fissidens crassipes* in one locality (Frahm, 1997). The vascular flora was also very poor, sometimes including *Potamogeton gramineus* in the freshly disturbed pebbly side-channels (Philippi, 1978), and much more frequently only including *Potamogeton lucens*, *P. pectinatus* and *Myriophyllum spicatum* in the older silted-up side-arms (Krause, 1981a).

Since the straightening of the river, the embankments have created stable substitution habitats on which

Table 2
Conditional relative frequencies of the characteristic vascular hydrophytes and algae of the floristic clusters

	Cluster				
	I	II	III	IV	V
Groenlandia densa	0.00	0.00	83.5	0.00	0.00
Elodea canadensis	0.00	0.00	66.5	71.5	0.00
Berula erecta	0.00	0.00	50.0	71.5	0.00
Hildenbrandia rivularis	0.00	0.00	28.5	16.5	0.00
Potamogeton friesii	0.00	40.0	50.0	28.5	0.00
Lemna trisulca	12.5	0.00	66.5	86.0	0.00
Potamogeton crispus	25.0	80.0	100	43.0	33.5
Callitriche obtusangula	37.5	20.0	66.5	100	100
Spirodella polyrhiza	100	100	66.5	14.0	0.00
Lemna minor	100	100	83.5	43.0	0.00
Elodea nuttallii	100	80.0	83.5	28.5	0.00
Sparganium emersum	62.5	0.00	50.0	14.0	0.00
Ceratophyllum demersum	100	40.0	66.6	14.5	0.00
Potamogeton berchtoldii	12.5	40.0	100	0.00	0.00
Potamogeton nodosus	50.0	20.0	16.5	0.00	0.00
Potamogeton pectinatus	100	40.0	100	0.00	0.00
Myriophyllum spicatum	87.5	0.00	100	0.00	0.00
Potamogeton perfoliatus	62.5	20.0	50.0	0.00	0.00
Lemna gibba	62.5	0.00	0.00	0.00	0.00
Potamogeton lucens	75.0	40.0	0.00	0.00	0.00

Roman numbers related to clusters are those described in text.

mountain species formerly characteristic of the rapids of the High Rhine, such as *Cinclidotus danubicus* and *C. riparius*, appeared and spread. Others, such as *Fissidens crassipes*, have spread extensively. Consequently, the straightening has caused the diversity of aquatic bryophytes to increase since the last century in the Middle and Lower Rhine (Frahm and Abst, 1993; Frahm, 1997), where about 15 aquatic bryophytes species are now commonly found. Vascular hydrophytes also spread after the management changes to the river (Schütz, 1993), finding optimal growth conditions in the side arms disconnected from the main river, at least partly fed by groundwater and consequently presenting much less variable discharges. Conversely, the short-lived Characeae characteristic of the former freshly disturbed side arms were affected by the decrease of river dynamics caused by the modification of the river. However, these Characeae are found in substitution habitats in gravel pits (Krause, 1969).

During the 20th century, the regulation of the river to facilitate the shipping, the construction of hydroelectric powerstations or even its canalization in France, has caused a great change in the water level. In the High Rhine, the increased water level upstream from the barrages has caused the disappearance of almost all the primary habitats. This has reduced niche diversity, reduced the area of water level variations and, as already shown in regulated rivers (Glime and Vitt, 1987; Englund et al., 1997), the aquatic bryophyte diversity. Some very rare species characteristic of the area, such as *Fissidens grandifrons* and *F. rufulus*, were on the verge of extinction (Philippi, 1961, 1968). Other, such as *Cinclidotus danubicus*, were able to adapt and to colonize habitats of substitution such as weirs. On the Upper Rhine, the water level variations were greatly reduced, so that strictly aquatic bryophytes such as *Octodiceras fontanum* appeared and spread extensively on the banks. On the other hand, species characteristic of variable water levels, like *Hyophila involuta*, were on the verge of extinction (Philippi, 1978). The increasing shipping was also a new factor limiting the development of the vascular hydrophyte flora. It has, in fact, been demonstrated that the abundance of vascular macrophytes is inversely proportional to the density of boat traffic (Murphy and Eaton, 1983). Boats physically damage the plants, which find refugia in sectors protected from shipping by isles or wharfs. Boat traffic also disturbs silt, which is held in suspension in the water and can then settle on the leaves of aquatic plants (Preston, 1995). The importance of silt in suspension on the aquatic flora is clearly shown in the upstream sector of the High Rhine. At Kilometric Point 0 in Konstanz, the waters flowing from Lake Constance, where the silt settles, are limpid. Hydrophyte assemblages there are consequently very diversified and very close to those described by Lauterborn (1910, 1916, 1917) including vascular plants with dominant *Myriophyllum spicatum*, *Zannichelia palustris*, *Ranunculus fluitans*, *Elodea canadensis*, *Potamogeton perfoliatus* and *P. crispus*, algae of good water quality like *Hildenbrandia rivularis* and *Chara globularis*. Downstream from the confluence with the river Thur, whose waters are very rich in deposits after strong rainfall, the turbidity of the Rhine waters increases, causing a decrease of the floristic assemblages.

In addition to niche structure and habitat conditions, it has been demonstrated that aquatic bryophyte (Frahm, 1974; Empain, 1977; Empain et al., 1980; Vrhosek et al., 1984), Characeae (Krause, 1981b) and vascular hydrophyte (Karpati, 1963; Haslam, 1982; Kohler, 1982; Wiegleb, 1984; Kohler and Schiele, 1985; Carbiener et al., 1990) assemblages segregate according to water quality. Along the Alpine Rhine, the progressive increase of the trophic level is shown by the appearance of species of eutrophic status like *Cinclidotus fontinaloides* whereas species of typically oligotrophic status such as *Palustriella commutata* disappear progressively in favour of *Cratoneuron filicinum* which has a much broader ecological range. Near the delta of the river in Lake Constance, the Austrian–Swiss industrial area causes eutrophication of the water shown by the increase of species of eutrophic status (*Cinclidotus riparius*, *Amblystegium riparium*) and the appearance of *Fissidens crassipes*. In the Upper Rhine, many of the good water quality species have decreased or even disappeared due to the severe water pollution levels reached in the 1970s. This is, for example, the case for *Jungermannia atrovirens*, which was known in many localities between Basel and Strasbourg at the beginning of the century (Philippi, 1968) and which is on the verge of extinction in the area. This good quality water flora has found refugia in the former side channels that have been disconnected from the main river and fed by groundwater since the canalization. This flora consequently shows affinities with that of the upstream sectors with good quality waters, in the upstream High Rhine or in the Alpine Rhine, and is the last regional relic of a flora that has disappeared from the main channel due to water pollution. Downstream from the area of Mannheim, the strongly eutrophic level only permits the presence of eutrophic pollution-tolerant species like *Octodiceras fontanum* that seems to appear upstream from Mannheim and becomes one of the dominant species from Mainz, hence the decrease of *Fissidens crassipes* occupying the same niche.

Vascular hydrophytes show a less obvious longitudinal zonation due to habitat conditions in the main channel. They show, however, a lateral zonation pattern in the side-arms of the main river, ranging from an oligotrophic level in exclusively groundwater-fed disconnected side-channels to a eutrophic level in still connected side-arms. The floristic clusters obtained in our typology can be compared to the vascular hydrophyte assemblages related to ammonium and phosphate concentrations in the Upper Rhine (Carbiener et al., 1990; Robach et al., 1996), i.e. a community of oligomesotrophic status with *Elodea canadensis*, *Berula erecta* and *Callitriche obtusangula* (cluster IV), a community of meso-eutrophic status including the former species and *Groenlandia densa* (cluster III), a community of eutrophic status with dominant *Potamogeton crispus* and *Elodea nuttallii* (cluster II) and a community of hypertrophic status characterized by the absence of species of meso-eutrophic status such as *Potamogeton friesii* and the abundance of polluo-tolerant species such as *Potamogeton lucens* and *P. nodosus* (cluster I). These communities consequently segregate along a lateral gradient of connectivity with the main river (Klein et al., 1995). However, the communities of phreatic springs located just behind the canalization dike (cluster V) exhibit a meso-eutrophic status, because the Rhine seeps through its gravelly bed and feeds the nearby watertable (Trémolières et al., 1993). Therefore, the meso-oligotrophic communities are more distant from the main river. Certain of these assemblages include very rare taxa (Klein et al., 1997), among them particular hybrids of pondweeds such as *Potamogeton xbennettii*. The hybrid pondweeds are often very localised and thus vulnerable to threats to particular sites. They, however, receive little attention from conservationists. The recognition of the intrinsic scientific interest of these plants by conservationists and an assessment of the extent to which their habitats are protected are now overdue (Preston, 1995).

5.2. Application to the conservation of the aquatic flora

Thanks to their particular habitat conditions and water quality, the disconnected side-channels provide refugia for communities of regulated river floodplains (Sedell et al., 1990). Groundwater-fed disconnected side-arms appear as reference systems for lowland oligotrophic hard waters. Nevertheless, a fundamental question persists, which is particularly well illustrated by the debate on the conservation of the secondary dry grasslands of the Upper Rhine valley (Brechtel et al., 1995; Coch, 1996; Neumann, 1996; Schenker, 1996; Reif, 1997): must the secondary habitats, that are refugia for relic biocenoses often appearing on the red lists, be preserved to the detriment of the ecosystem functionality? Conversely, must restoration ecology works, that can be defined as the return to the state before disturbance (Cairns and Heckman, 1996) or the repair of the damage caused to the diversity of the native ecosystems (Jackson et al., 1995), be undertaken in order to redynamize the alluvial ecosystems?

Hydraulic works are currently in progress in the Upper Rhine in order to retain the Rhine waters during the discharge peaks in lateral systems called "Polders" to preserve the areas downstream from the canalized Rhine from flooding and to redynamize the disconnected alluvial ecosystems. Very few data exist about the consequences of the functioning of the polders on the alluvial biocenoses (Burgeap, 1994). Polder Altenheim is the only one where ecological flooding is performed in the Upper Rhine. It is consequently the only place where the consequences of such flooding on the biocenoses can be assessed in order to define ecological optima of functioning in the other polders (Landesanstalt für Umweltschutz Baden-Württemberg, 1993). It was demonstrated that many shallow gravel riffles have been newly created or freed from mud deposits thanks to flooding and higher water velocity. This favoured the red alga *Hildenbrandia rivularis*. The eroded material was deposited downstream, creating islands quickly colonized by pioneer carabids (Coleoptera) that have developed a so-called flood behaviour (Siepe, 1994). In the groundwater-fed stretches, algae like *Chara* demonstrated their ability to recolonize quickly after flooding (Landesanstalt für Umweltschutz Baden-Württemberg, 1996).

However, very little attention has been paid to hydrophytes. In the 600 ha of Polder Erstein (France), the hydraulic works currently in progress will allow input discharges of surface waters up to 140 m3/s (Burgeap, 1994) during the retention of up to 7.8×10^6 m^3, whereas the annual mean discharge of the phreatic brooks is currently about 350 l/s (Sanchez-Perez and Maire, 1995). The floodpulse caused by the sudden input of surface water in the disconnected brooks will probably wash out most of the vascular hydrophytes and it is very likely that species with very low recolonization strategies will disappear in these conditions. In fact, it is well known that speed and recolonization potential are determinant in dynamic ecosystems. The growth rate in *Lemna minor*, for example, reaches 0.164 new plants per day but decreases to 0.0124 in *L. trisulca*, which confers to *L. minor* a proportionally greater potential of recolonization (Keddy, 1976). Disturbance caused by the functioning of the polder will consequently favour xenophytic species such as *Elodea nuttallii* or *Lemna minuta*, that have spread extensively in the valley since the 1970s (Wolff, 1980). It would thus be highly desirable to preserve from flooding the last oligotrophic brooks with their original hydrophyte assemblages. The brooks showing a tendency to silt up can be re-dynamized by ecological engineering works without disturbing the groundwater-fed streams. It has been demonstrated that replacing concrete pipes under paths by wooden bridges and the mechanical removal of silt by pumping out the mud enables the runoff to flow more quickly, with a consequent decrease in the duckweed carpets and the return of the red alga *Hildenbrandia rivularis* on the riffles (Klein et al., 1994). The choice of the sites of lateral flood retention should be focused on eutrophic and silted-up areas. In the areas including flowing groundwater-fed streams that have already been designed as areas of flood retention, the hydraulic works should allow as far as possible the preservation of these streams by only permitting the input of surface water upstream from the silted-up brooks.

6. Conclusion

The human activities in the Rhine valley originally led to an increase in its aquatic flora. Mountain bryophytes spread from the High Rhine to the dowstream sectors, finding substitution habitats on the embankments of the modified river. The diversity of vascular hydrophytes also increased in the side-arms disconnected from the main river, exhibiting much less variable discharges and silt deposits. Later, water pollution led to a severe decrease in the diversity of hydrophytes. Lateral disconnected side arms mostly fed by groundwater or gravel pits thus became refugia for the hydroflora. This aquatic flora has not been adequately considered in the recent projects for the ecological restoration of the alluvial floodplain. We propose a compromise for redynamizing the eutrophic silted-up areas by reconnecting them to the main channel and conserving the oligotrophic side-channels as plant refugia by ecological engineering to maintain flowing water in them. It is from these refugia that the main channel, whose water quality has been improving for a decade (Malle, 1996; Tittizer and Krebs, 1996), could be recolonized by its primary flora.

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