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ScienceDirect
Limnologica 37 (2007) 290–302
LIMNOLOGICA
www.elsevier.de/limno

The impact of environmental factors on the distribution pattern of aquatic plants along the Danube River corridor (Slovakia)

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Received 26 March 2007; received in revised form 19 June 2007; accepted 12 July 2007

Abstract

The aim of the study was to evaluate pattern of the aquatic macrophyte species distribution along the Danube fluvial corridor in Slovakia, and to identify the impact of environmental abiotic parameters on macrophyte species diversity. Field sampling was performed in the period 1999–2005 from the boat. Aquatic habitats were divided into 365 survey unit (SU). The survey of aquatic macrophytes and abiotic parameters followed the European standard approach EN 144184 2003. The plant mass estimate (PME – a semi-quantitative estimation of the amount of individual species in a SU, which takes into account three-dimensional development of plant stands) was estimated according to a five-point-scale in each SU; environmental pattern, were assessed over six abiotic parameters (river km, bank type, sediment type, flow velocity class, land-use type, and heavily man-modified water bodies). Altogether, four hydrologic connectivity types of aquatic habitats were distinguished: the Danube River, Open Arms, Separated Arms, and Seepage Water-bodies.

In total, 54 aquatic macrophytes were recorded for the whole data set of the Danube fluvial corridor. The PME data of true aquatic macrophytes and the length of SUs created a basis for numerical derivates, relative plant mass (RPM), mean mass indices (MMT, MMO) and the distribution ratio (*d*).

The results correspond with comparable studies on this topic: the highest macrophytes species diversity occurred in Separated Arms. On the contrary, macrophytes had the lowest richness in the Danube River main channel, although their diversity was slightly higher in heavily man-modified water bodies (such as the hydropower plant's reservoir and the abandoned main channel of the so-called Old Danube). Our results suggest that the lateral connectivity types of the river water bodies, primarily characterised by different hydrologic dynamics and human impact expressed as land-use types are responsible for the variability of aquatic macrophyte assemblages along the Danube corridor in Slovakia.

Keywords: Macrophytes; Abiotic parameters; Hydrologic connectivity; DCA

Introduction

The macrophyte species composition and abundance correspond to environmental factors in rivers across Europe (Janauer & Dokulil, 2006; Pinto, Morais, Ilhéu, & Sandin, 2006). The relationships between morphological, hydrological, physical, and water quality patterns of riverine systems and the aquatic macrophytes distribution have widely been investigated, although, mainly at the regional level (Baattrup-Pedersen & Riis, 1999; Hrivnák, Ot'ahel'ová, & Jarolímek, 2006; Kohler & Schneider, 2003; Kohler, Vollrath, & Beisl, 1971;

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0075-9511/$ - see front matter
doi:10.1016/j.limno.2007.07.003

Onaindia, de Bikuña, & Benito, 1996; Riis & Sand-Jensen, 2002; Sabbatini, Murphy, & Irigoyen, 1998; Thiébaut & Müller, 1999). Aquatic macrophytes, which play an important role in fluvial corridors, are becoming a matter of particular concern for the scientific and economic sphere in relation to the current requirement of the Water Framework Directive to use aquatic macrophytes as biological elements for the assessment of the ecological status of rivers (Meilinger, Schneider, & Melzer, 2005; Onaindia, Amezaga, Garbisu, & García-Bikuña, 2005; Schaumburg et al., 2004; WFD, 2000). At present, river corridors with associated floodplain water bodies are a focus of biodiversity studies in the European landscape (Janauer, 2004). In many rivers, anthropogenic impacts, such as, e.g., the embankment, have negatively impeded fluvial processes responsible for creating new wetlands (e.g. flooding, channels migration); thus, the preservation and restoration of relic wetlands have actually become the only remaining option in terms of environmental management (Amoros, Bornette, & Henry, 2000).

The Danube is the second longest river in Europe. Although its natural course has strongly been altered by human activities, the Danube still exhibits a fair amount (51%) of free-flowing sections. Therefore, the need for more effort in floodplain research is still pressing (Bloesch, 2003). The topic of aquatic macrophyte vegetation has been discussed in numerous contributions from different countries (Adamec, Husák, Janauer, & Ot'ahel'ová, 1993; Janauer & Wychera, 2000; Ot'ahel'ová, 1980; Pall & Janauer, 1995; Pall, Rath, & Janauer, 1996; Rath, 1987). Some of them reported an increase of hydrophytes associated with the construction of the Gabčíkovo Hydropower Plant in the middle Danube reaches (Ot'ahel'ová & Valachovič, 2002; Rath, 1997). Conversely, decreased species richness and simplified structure of submerged vegetation have been registered in the Lower Danube in response to eutrophication effects during two successive decades since 1980 (Cristofor et al., 2003). Lately, many publications (Dorotovičová, 2005; Janauer & Pall, 2003; Janauer & Steták, 2003; Janauer, Vukov, & Igić, 2003, Ot'ahel'ová & Valachovič, 2003, 2006; Rath, Janauer, Pall, & Berczik, 2003; Sârbu, 2003; Schütz, Veit, & Kohler, 2006; Vukov, Igić, Boža, Anačkov, & Janauer, 2006) on the floristic composition and distribution of aquatic macrophytes from nearly all Danube countries, carried out using the standard methods (Janauer, 2003; Kohler, 1978; Kohler & Janauer, 1995; EN 14184 2003), have appeared as a part of the MIDCC project (www.midcc.at). The aim of our paper was: (i) to assess the patterns of species diversity and distribution of aquatic macrophytes in different habitats of the Danube fluvial corridor in Slovakia, (ii) to determine the effect of selected environmental parameters on the macrophyte species composition and abundance.

Study area

Out of the total Danube length of 2850 km, the Slovak reach is 172 km long, 7.5 km of the right-side bank border Austria and 142 km are the border with Hungary. The Danube enters Slovakia from Austria at 1880 river km (rkm) and flows into Hungary at 1708 rkm. The river average discharge in Bratislava is $2025\,m^3\,s^{-1}$, the minimum and maximum discharges vary between 560 and $10400\,m^3\,s^{-1}$. Studied habitats had neutral to slight alkaline pH water reaction. Climatic conditions in the area are warm (July mean temperature is above 20 °C) and very dry (mean annual precipitation totals from 500 to 550 mm). Winters are mild (Lapin, Faško, Melo, Šťastný, & Tomlain, 2002).

The altitude range from 103 to 130 m and are typical for lowland fluvial plains. During the Quaternary period, the aggradations of gravel and sand flattened the Danube's gradient between Bratislava city and Komárno. The network of river arms, the so-called "Inland Delta", has been formed there. Dynamic morphological changes of the Danube riverbed between the 16th and 19th centuries favoured the development of a broad range of new habitats – from cut-off arms, through floodplain forests to xerothermic habitats (Pišút, 2006). In the 1980's, the Gabčíkovo Hydropower Project was commenced, starting to operate in 1993. As a result, the Čunovo Reservoir, the adjacent seepage canals, the abandoned bed of the main channel so-called Old Danube – and the altered anabranch system came into existence (Kocinger, Mucha, Hlavatý, & Kučárová, 1999).

Based on hydrologic connectivity and hydrodynamics, we distinguished four major types of current aquatic habitats along the Slovak part of the Danube river corridor in line with their distinctive abiotic features. This approach is generally used in the Danube River catchment (Ot'ahel'ová & Valachovič, 2003, 2006; Pall et al., 1996; www.midcc.at).

- *Danube River* (eupotamal) – the present main channel (from 1880 to 1708 rkm) with the Čunovo Reservoir (also called Hrušov Reservoir) and the Old Danube (1841–1811 rkm);
- *Open Arms* (parapotamal) – the river branches, during periods of mean Danube discharge permanently or temporarily connected with the main channel through surface water;
- *Separated Arms* (plesiopotamal) – backwaters, normally isolated during the baseline river, supplied by groundwater connection, while short-term connections are possible during high floods;

- *Seepage Water-bodies* – artificial seepage canals and pit lakes along the Danube channel.

Methods

Sampling procedure

Field sampling was performed in the summers of 1999–2005 from the boat. The assessment of aquatic macrophytes and abiotic parameters followed a standard approach (Janauer, 2003; EN 14184 2003). Studied aquatic habitats, with a total length of 276 650 m, were divided into contiguous survey units (SU) with ecologic homogeneity, apart from the main channels border bank, where SUs were usually of 1000 m length (Table 1). The SUs in the main channel are separated for the left and right banks, as the central part of the river is without any vegetation. In the other water bodies types the SUs were assessed for the whole width of the channels without differentiation between the two banks. The plant mass estimate (PME – the amount of individual species in a SU, which takes into account three-dimensional development of plant stands) was estimated according to a five-point-scale (1 – rare, 2 – occasional, 3 – frequent, 4 – abundant, 5 – very abundant) in each SU.

The prevailing type of following six abiotic parameters was evaluated for each SU: river km (distance from the river outfall), bank (artificial material including rip–rap structure >6.3 cm; gravel 0.2–6.3 cm; sand – 0.063–0.2 cm; fine inorganic substrate <0.063 cm), sediment type (the substrate, where the plants were growing – artificial material including rip–rap structure; gravel; sand; fine substrate), flow velocity class (stagnant, low flow velocity – from just visible to ca. 30 cm s^{-1}; medium flow velocity ca. 35–65 cm s^{-1}; high flow velocity more than 70 cm s^{-1}), CORINE land-use type adjacent to the banks (only four basic groups were used – settlement and transport; agricultural land; forest including shrub; wetland), heavily man-modified water bodies (reservoirs, ports, weirs, canals and pits), and four hydrologic connectivity types of aquatic habitats (Danube River; Open Arms; Separated Arms; Seepage Water-bodies; for details see Study area). The study was based on the field data from 365 SUs of aquatic habitats including earlier published data from the Danube River corridor (Jursa & Ot'ahel'ová, 2005; Ot'ahel'ová & Valachovič, 2003, 2006).

Table 1. Size characteristics and abiotic parameters of surveyed aquatic habitats of the Danube fluvial corridor (the prevailing parameters are given in bold)

Abiotic parameters	Codes in DCA	Danube River	Open Arms	Separated Arms	Seepage Waters
Surveyed length (km)		194.9	27.6	23.5	30.7
Number of SU		190.0	57.0	56.0	62.0
Average length of SU (m)		1026.0	485.0	419.0	495.0
Bank structure in %					
Artificial material	1	**54.1**	16.7	12.7	0.4
Gravel	2	26.7	18.2	14.3	**99.6**
Sand	3	7.7	5.1	3.3	–
Fine substrate	4	11.5	**60.0**	**69.7**	–
Sediment type in %					
Artificial material	1	2.6	–	2.5	–
Gravel	2	**63.5**	15.1	35.6	45.6
Sand	3	11.8	**78.9**	3.3	–
Fine substrate	4	22.1	6.0	**58.6**	**54.4**
Land-use type in %					
Settlement and transport	1	28.7	27.6	28.3	**100.0**
Agricultural land	2	9.8	–	3.4	–
Forest	3	**51.1**	**72.4**	**68.3**	–
Wetlands	4	10.4	–	–	–
Flow class in %					
Stagnant	1	–	29.8	**82.6**	**56.3**
Low flow	2	5.5	**64.1**	17.4	40.3
Medium flow	3	39.7	6.1	–	3.4
High flow	4	**54.8**	–	–	–

Data analysis

The PME data for true aquatic macrophytes and the SUs length created a basis for numerical derivates, relative plant mass (RPM – the percentage of relative "plant quantity"of each species weighted by the river section length in the order of dominance) and mean mass indices (MMO – the abundance index of an individual species with respect to the SUs where it occurs; MMT – the abundance index of this species with regard to the full length of the river investigated), and the distribution ratio ("*d*" is the ratio of two former parameters ranging from 0 to 1). Calculation of RPM, MMT, MMO, *d*, and proportion of abiotic parameters were computed on-line on the website (www.midcc.at) for each habitat type. The MMT index was used for the calculation of the Shannon's index of species diversity (H_s; Eq. (1)) and equitability (E; Eq. (2)) (Whittaker, 1972). The nomenclature of plant species follows Marhold and Hindák (1998), the categories of threat are classified according to Feráková, Maglocký, and Marhold (2001), Hindák and Hindáková (2001), and Kubinská, Janovicová, and Šoltés (2001). Filamentous green algae were grouped as one "taxon" Algae filamentous. Species abbreviations are given in Table 2.

The CANOCO 4.5 for Windows package (Ter Braak & Šmilauer, 2002) was used for running Detrended Correspondence Analysis (DCA). PME values of all detected macrophytes (including true aquatic macrophytes and helophytes) were processed in the analysis. The gradient length for the first DCA axis of 6.871 indicated that the unimodal model was suitable for the analysis. Rare species were downweighted and 21 outlier samples were omitted. Post hoc correlation of unconstrained axes with the environmental variables and correlation among variables were used.

$$H_s = -\sum_{i=1}^{s} N_i \ln N_i, \tag{1}$$

$$E = \frac{H_s}{\ln s}, \tag{2}$$

where H_s is the species diversity, E the equitability, N_i the quantity of the species i/total quantity of all species, s the total number of taxa in the community.

Results

Abiotic parameters

The hydrological connectivity types, primarily characterised by different flow velocity rates, determine the morphometry of water bodies and the use of the neighbouring land (Table 1).

Table 2. Species list, abbreviations and categories of threat of aquatic macrophytes, recorded in the habitats along the Slovak reaches of the Danube River corridor (X – species occurrence, MC – main channel, OD – Old Danube River, CR – Čunovo Reservoir, categories of threat: CR – critically endangered, EN – endangered, VU – vulnerable, LR – lower risk, § – protected by law)

Species	Abbrev.	Danube R.			Side Arms	Separated Arms	Seepage Water-bodies	Threat
		MC	OD	CR				
Alisma gramineum	Ali gra			X				VU
Apium repens	Api rep						X	CR §
Batrachium circinatum	Bat cir				X	X	X	
Batrachium trichophyllum	Bat tri		X		X	X	X	
Berula erecta	Ber ere					X		VU
Butomus umbellatus	But umb		X		X	X		VU
Callitriche cophocarpa	Call cop				X	X	X	LR
Ceratophyllum demersum	Cer dem	X	X	X	X	X		
Eleocharis acicularis	Ele aci		X		X	X	X	
Elodea canadensis	Elo can						X	
Elodea nuttallii	Elo nut	X	X	X	X	X	X	
Groenlandia densa	Gro den						X	EN §
Hippuris vulgaris	Hip vul					X	X	EN §
Hydrocharis morsus-ranae	Hyd mor				X	X		

Table 2. (*continued*)

Species	Abbrev.	Danube R.			Side Arms	Separated Arms	Seepage Water-bodies	Threat
		MC	OD	CR				
Lemna minor	Lem min	X		X	X	X	X	
Lemna trisulca	Lem tri				X	X		
Myosotis scorpioides	Myo sco				X	X	X	
Myriophyllum spicatum	Myr spi	X	X		X	X	X	
Myriophyllum verticillatum	Myr ver					X	X	VU §
Najas marina	Naj mar	X		X	X	X		LR
Najas minor	Naj min				X	X		VU
Nuphar lutea	Nup lut				X	X		VU
Nymphaea alba	Nym alb					X		VU §
Nymphoides peltata	Nym pel					X		EN §
Polygonum amphibium	Pol amp		X		X	X		
Potamogeton acutifolius	Pot acu					X		VU §
Potamogeton crispus	Pot cri	X		X	X	X	X	
Potamogeton lucens	Pot luc					X	X	
Potamogeton nodosus	Pot nod	X		X	X	X	X	LR
Potamogeton pectinatus	Pot pec	X	X	X	X	X	X	
Potamogeton perfoliatus	Pot per	X	X	X	X	X	X	LR
Potamogeton pusillus	Pot pus		X	X	X	X	X	
Potamogeton trichoides	Pot tri	X			X			VU
Rorippa amphibia	Ror amp		X		X	X		
Sagittaria sagittifolia	Sag sag				X	X		LR
Salvinia natans	Sal nat					X		LR §
Schoenoplectus triqueter	Sch tri			X	X	X		CR §
Sparganium emersum	Spa eme					X	X	
Sparganium erectum	Spa ere					X		
Spirodela polyrhiza	Spi pol	X			X	X		
Stratiotes aloides	Stra alo					X		EN §
Trapa natans	Tra nat					X		VU §
Utricularia vulgaris	Utr vul					X	X	VU §
Veronica anagallis-aquatica	Ver ana		X		X		X	
Veronica beccabunga	Ver bec		X		X			
Zannichellia palustris	Zan pal	X	X	X	X		X	
Chara globularis	Cha glo					X	X	EN
Chara hispida	Cha his						X	EN
Chara vulgaris	Cha vul					X	X	EN
Nitella syncarpa	Nit syn						X	EN
Nitellopsis obtusa	Nit obt					X		EN
Cinclidotus riparius	Cin rip	X	X		X	X		LR
Fontinalis antipyretica	Fon ant						X	
Riccia fluitans	Ric flu					X		VU
Algae filamentous	alg fil	X	X	X	X	X	X	

Regarding the flow class, in the *Danube River* the high flow predominates, followed by the medium flow. Bank structure belongs to the most variable parameters: more than a half of bank lengths are reinforced by rip–rap or other artificial material. Gravel is a dominating sediment type; only one-third of SUs is characterised by fine inorganic sediment and sand. Land-use types are diversified; alluvial forest, however, prevails in the riverine area.

Open Arms comprise most variable types of flow rates. Some arms are permanently connected with the main channel, other establish lateral connectivity temporarily, in relation to the current hydrological situation on the Danube River, or water management. However, low flow conditions prevail during the vegetation period. Fine substrate material is spread out over the half of the riverbank area and sand becomes a dominant sediment type. Open Arms are mainly surrounded by forest; however, one-third of SUs are situated in urban area.

Separated Arms are characterised by the prevailingly stagnant water level, responsible for the dominance of fine-grained sediment in the bottom and riverbanks. Riparian forest prevails along adjacent banks.

Abiotic parameters are rather uniform in *Seepage Water-bodies*, with gravel-covered banks and sediment type being half fine substrate, half gravel. Stagnant and low flow conditions characterise these artificial water bodies. Only one land-use type – "settlement and transport" was recorded.

Species diversity and distribution

In total, 54 aquatic macrophytes, out of which 46 vascular plants, three bryophyte species, four stoneworts – Charophyceae, and filamentous algae were recorded in the whole data set of the Danube fluvial corridor. The Shannon's diversity index was equal to 5.18 and the Equitability to 0.90. *Elodea nuttallii* (RPM = 12.6%, $d = 0.12$, MMT = 1.2, MMO = 2.4) was the most frequent vascular plant species, followed by *Zannichellia palustris* (RPM = 10.6%, $d = 0.13$, MMT = 1.1, MMO = 2.2) and some other species such as *Potamogeton pectinatus*, *Potamogeton nodosus*, *Myriophyllum spicatum*, and *Ceratophyllum demersum*; no ubiquitous taxa ($d > 0.5$) were identified along the Danube corridor in Slovakia. Only low values of plant mass were observed. Four types of habitats with different lateral connectivity and hydrodynamics provided distinctive features of macrophyte abundance and distribution (Figs. 1 and 2).

The Danube River, including the main channel, the Old Danube and the Čunovo Reservoir, had the lowest rates of species diversity and equitability ($H_s = 4.30$, $E = 0.94$). Out of a total number of 24 aquatic macrophytes, *Z. palustris* was dominant, still exhibiting low mean abundance (RPM = 36.9%, MMT = 1.1), followed by the moss species *Cinclidotus riparius*. The RPM values of other vascular plants such as *Eleocharis acicularis*, *P. pectinatus*, *P. nodosus*, and *M. spicatum* ranged from 3% to 8%, developing a clumped distribution. Other macrophytes occurred very rarely, though *E. nuttallii*, *P. pectinatus*, *Potamogeton perfoliatus*, *Z. palustris*, and *C. demersum*, were found in all subhabitats, e.g., Old Danube, Čunovo Reservoir, and the main channel of the Danube River. Conversely, fertile populations of *Alisma gramineum* (MMO = 2.25*)* survived only in the Čunovo Reservoir.

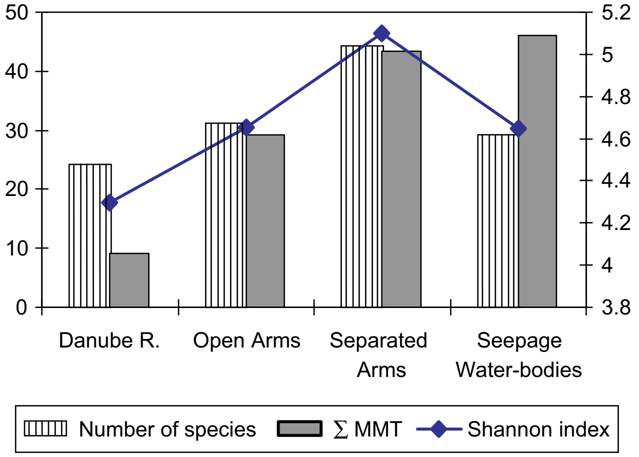

Fig. 1. Species diversity and mean mass sums (MMT) of aquatic plants along the Danube River corridor in Slovakia.

Altogether, 31 aquatic species were identified in *Open Arms*. The Shannon's diversity index value was $H_s = 4.65$, and the Equitability index $E = 0.94$, respectively. Most frequent was *E. nuttallii* (RPM = 28.9%, $d = 0.83$), followed by *P. perfoliatus*, *P. pectinatus*, *M. spicatum*, and *C. demersum*; other species reached RPM < 5%. The values of mean mass indices were generally low, except for *E. nuttallii* (MMT = 2.59, MMO = 2.76). Some species, such as *Najas minor*, occurred locally (MMO = 2.43, $d = 0.05$).

The presence of 44 aquatic species, the Shannon's index $H_s = 5.10$ and equitability index $E = 0.94$, featured the highest species diversity in *Separated Arms. M. spicatum* (RPM = 21.5%, MMT = 2.90, $d = 0.88$) was a dominant species, RPM values of *P. nodosus*, *C. demersum*, *Nymphaea alba*, *Batrachium circinatum*, and filamentous algae varied from 6% to 10%. Only three species, *M. spicatum*, *P. nodosus*, *C. demersum*, and filamentous algae slightly exceeded the MMT = 2, however, the MMO > 2 was recorded for 19 species. For example, *Stratiotes aloides* reached the MMO = 5, but was distributed only locally ($d = 0.01$).

In *Seepage Water-bodies*, 29 species, the Shannon's index $H_s = 4.65$ and equitability index $E = 0.96$ were recorded. Stonewort reached the highest RPM and MMT values, although they were distributed incoherently

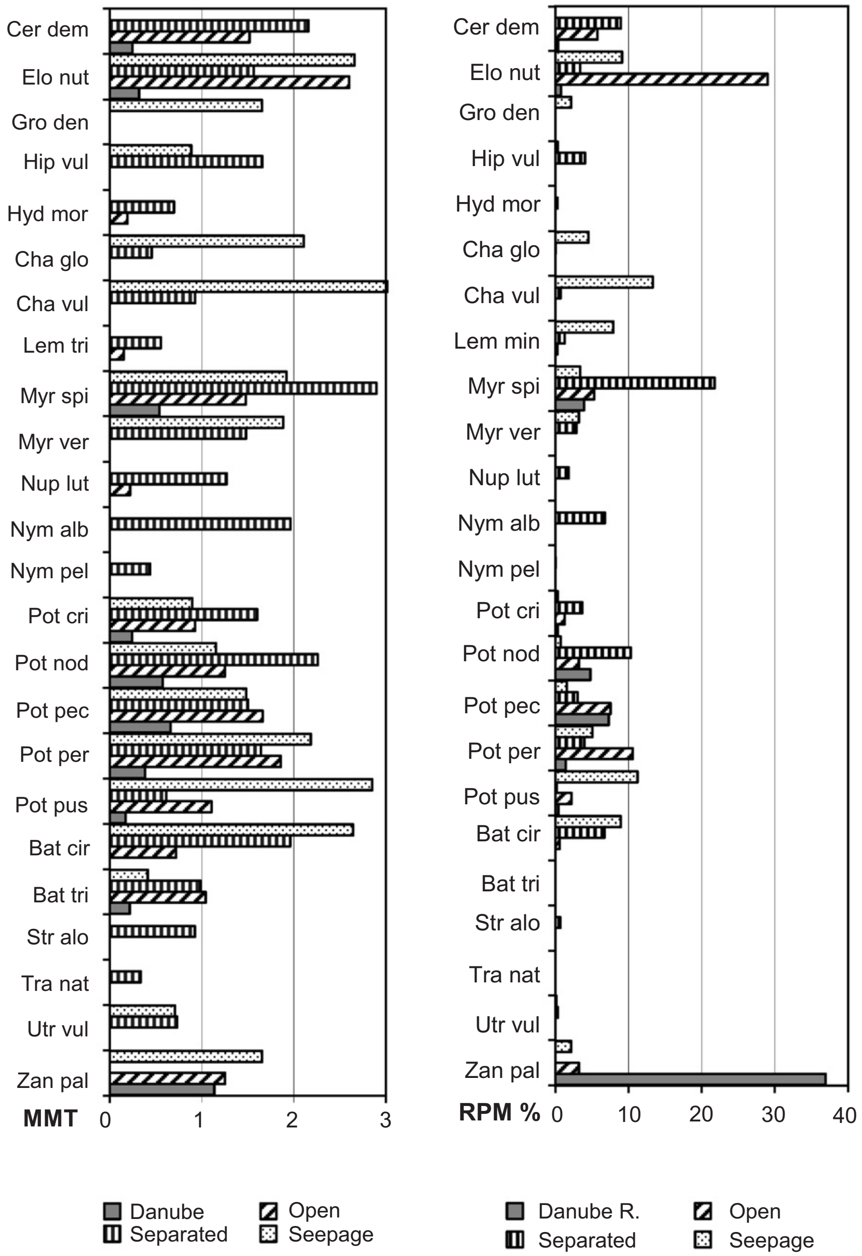

Fig. 2. Mean mass total (MMT) and relative plant mass (RPM) of selected macrophytes in aquatic habitats: Danube River, Open Arm, Separated Arm, and Seepage Water-body. Species abbreviations are explained in Table 2.

(*Chara vulgaris* RPM = 13.3%, MMT = 3.01, $d = 0.29$). The RPM values of *Potamogeton pusillus* and *E. nuttallii* fluctuated from 11.2% to 9.1%; they exhibited larger distribution ($d > 0.5$). Beside stoneworts, *Elodea canadensis*, *E. nuttallii*, *P. pusillus*, *B. circinatum* and filamentous algae exceeded the MMO > 3.

Connectivity types and environmental gradients

The first two DCA axes explain 8.5% and 5.2% of the species data set variability and 30.2% and 13.6% of the species environmental relation, respectively. Connectivity types manifested the following sequence along the first DCA axis: the Danube River, Open Arms, Separated Arms, with the gradient eventually finalising in Seepage Waters (Fig. 3). The first two habitats are mixed and closely relate with each other in species composition. The Seepage Water-bodies and Separated Arms are floristically better differentiated. Among aquatic macrophytes, *Apium repens*, *Groenlandia densa*, *Chara hispida*, *Nitella syncarpa*, and *Fontinalis antipyretica* were the only recorded in Seepage Waters, conversely *N. alba*, *Nymphoides peltata*, *S. aloides*, *Trapa natans*, *Nitellopsis obtusa* and *Riccia fluitans* – in Separated Arms (Table 2).

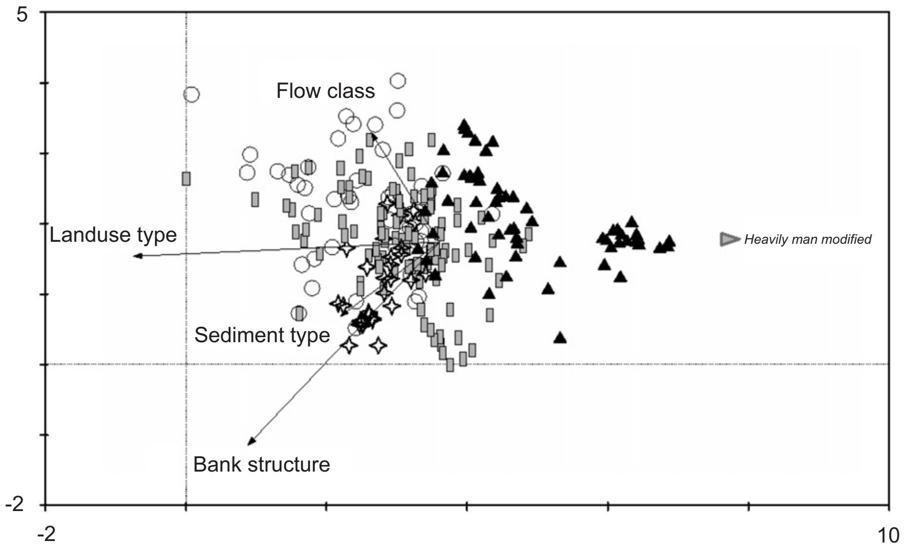

Fig. 3. DCA ordination diagram of surveyed units and post hoc correlated environmental variables (empty circle – Danube River, full rectangle – Open Arm, empty star – Separated Arm, full triangle – Seepage Water-body).

Among the studied abiotic variables, the land-use type (post hoc correlation with the first DCA axis −0.65) most comprehensively explained the main environmental gradient reflecting the intensity of human impact upon the exploited river habitats and neighbouring landscape (Fig. 3). Samples were arranged from relatively natural to strongly man-modified habitats. The second DCA axis is largely in line with the Bank structure (−0.41).

Discussion

The Danube passes through Slovakia in its middle reaches. However, the length of the Danube main channel of only 172 km is characterised by high spatial heterogeneity of abiotic environment and biodiversity (Bulánková & Krno, 2006; Lisický & Mucha, 2003).

In total, 54 aquatic macrophytes across studied habitats of Slovakia's fluvial corridor were recorded in the period 1999–2005. The species assemblage in this river reaches differs from the Upper Danube in Germany, where *Ranunculus fluitans* and *F. antipyretica* are abundant, mainly in fast-flowing channelised sections. However, the chain of reservoirs induces the succession of *Nuphar lutea* and narrow-leaved pondweeds (Schütz et al., 2006). The reaches of the Middle and Lower Danube and the Danube Delta feature a similar floristic structure. Only some thermophilous species, such as *Azolla filiculoides* were found downstream from Slovakia to the south Hungary (Janauer & Steták, 2003; Köder, Sipos, Zeltner, & Kohler, 1999) occurring in water bodies across the Middle and Lower Danube. However, *A. filiculoides* was found in the Slovak tributary of the Danube – in the impoundment of the Váh River. Also, *Vallisneria spiralis* is distributed in Serbia (Vukov et al., 2006) and Bulgaria (Valchev, Georgiev, Ivanova, Tsoneva, & Janauer, 2006), and Romania (Sârbu, Janauer, Exler, & Filzmoser, 2006). It was also recorded in Austria, though as a neophyte species (Baart et al., 2006). The alien species *Cabomba caroliniana* invades canals (Köder et al., 1999) and the main channel (Janauer & Steták, 2003) in Hungary. An endangered species, *Marsilea quadrifolia*, was found in a floodplain lake in Bulgaria (Valchev et al., 2006). Based on the preliminary data of the MIDCC project, Janauer et al. (2006) refer to *C. demersum*, *P. pectinatus*, and *Butomus umbellatus* as the most frequent species in the entire Danube River corridor. Wide distribution show both alien invaders *E. canadensis* and *E. nuttallii*, which are rapidly spreading along the whole Danube in last decades.

Recent spacing of aquatic habitats, their hydrodynamics and physical traits had mainly developed in response to the management, e.g., the riverbed regulation for flood protection, navigation, and hydropower plants engineering. Main pattern of aquatic macrophytes is closely related to morpho-hydrology and trophic state of habitats (Ludovisi, Pandolfi, & Taticchi, 2004), which change in response to the regulation of the anastomosis of rivers (Chauhan & Gopal, 2005; Janauer, 2001). The typology of the former channels based on their connectivity with the river and groundwater (permanent connection, temporal connection and connection through river flood) in relation to plant species richness was used for the Rhône River in France (Bornette, Amoros, & Lamouroux, 1998). Spatial connectivity along and between the river is considered as the most important factor in shaping aquatic vascular plants assemblages of lowland rivers in England (Demars & Harper, 2005) and in the Danube River as well (Baart et al., 2006; Ot'ahel'ová & Valachovič, 2006; Pall et al., 1996).

Land use of riparian zone and bank structure are the most important parameters explaining variance in the composition of macrophyte community in Slovenian watercourses (Kuhar, Šraj-Kržič, Germ, Urbanc-Berčič, & Gaberščik, 2006) and this corresponds with our investigation. Janauer and Exler (2004) describe the urban and industrial areas as suitable habitats especially for the submersed species along the Danube corridor. Both land use and bank structure parameters indicate human impact in the landscape surrounding the river corridor. Large anthropogenic effects on hydrology are associated with the construction of dams, and diversions for hydroelectricity and agricultural purposes. This probably results in local enrichment of macrophyte productivity through the deposition of fertile sediment and enhanced availability of dissolved nutrients (cf. Lacoul & Freedman, 2006). The degradation of natural habitats has been cited as a cause of loss of native species (Deil, 2005) and the invasion of alien species (Di Nino, Thiébaut, & Müller, 2005; Hussner & Losch, 2005).

The hydrological connectivity type of aquatic habitats and utilisation of surrounding country (land-use type) explain the main environmental gradient along the Danube corridor in Slovakia: studied aquatic habitats were arranged through (i) Danube River and Open Arms to Separated Arms and Seepage Waters, (ii) natural to man-modified habitats (Fig. 3). The results correspond with four main types of connectivity, which were arbitrarily distinguished at the beginning of our study.

Danube River is characterised by the lowest values of both species diversity and mean value of MMT, due to high flow velocity, prevailing gravel sediment, and artificial bank structure (see Tables 1 and 2; Fig. 1). In general, high current velocity, coarse-grained material of banks and bottom make the environment unsuitable for vascular aquatic plants (Madsen, Chambers, James, Koch, & Westlake, 2001). Some rhizophytes, such as *Z. palustris*, *Potamogeton* species, *M. spicatum*, etc. sporadically occupy sheltered microhabitats of slow flow velocity with silt located near the mouths of tributaries, or the arms of the Danube main channel. In the same or similar sites, pleustophytes (free-floating species), such as duckweeds and *C. demersum*, were recorded only scarcely. Only the moss species *C. riparius* colonised washed boulders of rip–rap zone, owing to rhizoids that enable it to attach. Janauer (2001) described similar moss patches on regulated Danube banks in Austria, where, prior to the regulation, vascular plants grew on the fine-coursed substrate.

In our investigation, the highest species richness of 16 vascular hydrophytes was recorded in the Old Danube, due to the flow rate reduction after the water diversion in the hydropower plant's bypass canal in 1992. Practically no aquatic macrophytes before this technical adjustment occurred there, only a small clump of *P. pectinatus* was found at 1830 river km in 1991 (Ot'ahel'ová & Valachovič, 2002). Similar results from the macrophyte survey were obtained along the right, Hungarian, bank of the Old Danube (Rath et al., 2003) using the same method. *Z. palustris* was the most widespread aquatic plant that formed a submerged carpet on thin deposits of mud along the shallow littoral. Only low occurrence and sparse distribution of other macrophytes, such as *P. pectinatus*, *P. perfoliatus*, and *E. nuttallii* was generally recorded. The Čunovo Reservoir**,** which construction was completed in 1993, had successfully been colonised by macrophytes (Ot'ahel'ová & Valachovič, 2002). However, they preferred the left-side upper reaches of the impoundment with a shallow littoral covered with deposits of fine sediments due to decreased water velocity. After the pioneering *Z. palustris* and *E. nuttallii*, *P. nodosus* currently becomes abundant. Similarly, favourable habitats for macrophyte colonisation have developed in the impoundments of hydropower plants in Austria (Janauer, 2001; Janauer & Pall, 2003; Schmidt, Straif, Waidbacher, & Janauer, 2006), and in the Danube lower reaches in Serbia (Vukov, Anačkov, Igic, & Janauer, 2004).

Open Arms followed the Danube River in species diversity and had similar species composition (Fig. 1, Table 2). Alien species *E. nuttallii* frequently occurred in some of them, mainly in heavily modified arms (e.g. harbours) located in urban areas. A semi-natural network of arms varied in morphological patterns and hydrodynamics. Since 1993, a special inlet structure ensures flow continuity and controls water level in the anabranch system on the left bank of the Old Danube River. A large-scale of flow velocities and water depths in river branches, with the velocity as fast as $1\,\mathrm{m\,s^{-1}}$ at some places, to near stagnant water in side branches, and stagnant water in old dead branches supplied with groundwater distinguishes these arms (Lisický & Mucha, 2003). Spatial boundaries between both types of Open and Separated Arms have a temporal character. Species composition in Open Arms is generally similar to those in the Danube River, but plant species abundance, displayed by mean value of MMT, is rather higher (see Table 2; Fig. 1). Submerged rhizophytes dominate: patches of pondweeds are common; *E. nuttallii* is ubiquitous ($d = 0.83$).

Some *Separated Arms* are located outside the flood-protection dam. The majority, however, remained in the inundation area developing in response to fluvial deposits or decreased water level. Only during high floods, such as in 2002, they establish connectivity with the main channel. This occasional flood disturbance is nevertheless very important because it slows down the vegetation succession, which may lead to the decline of aquatic macrophyte species richness and diversity (Bornette & Amoros, 1996). Highest species richness and diversity is generally known from these separated habitats (cf. Bornette et al., 1998; Dawson & Szoszkiewicz, 1999; Ludovisi et al., 2004; Ward & Tockner, 2001), what correspond with our results (Fig. 1). Floating-leaved species, such as *N. alba*, *N. peltata*, *Salvinia natans*, *S. aloides*, and *T. natans*, were only recorded in lentic conditions. Eutrophic conditions also favoured filamentous algal communities. Many species have shown the clumped distribution here. As to endangered species list, this type of habitat is of special value (Table 2).

Surveyed *Seepage* canals and pit lakes, built in 1979–1992, relate to the Gabčíkovo Hydropower Plant construction. Water supply is maintained through the infiltration of relatively cold groundwater, which is either stagnant or of low flow velocity, has good transparency and is only slightly eutrophic. This new habitat provides a niche for the plant succession. Already in 1999, 25 aquatic macrophytes were recorded in one of the canals (Ot'ahel'ová & Valachovič, 2003) and the number of species continued to increase: 29 macrophytes were found in the canals in 2001.The abundance of species was relatively high as it is indicated by the MMT mean value (Fig. 1). Species assemblage in Seepage Water-bodies is different enough comparing to others habitats (Table 2). Most frequent are stoneworts (Characeae*)*, which usually occur as pioneer macro-algae in newly dug ecosystems supplied with groundwater (Bornette & Arens, 2002; Lambert-Servien, Clemenceau1, Gabory, Douillard, & Haury, 2006; van Geest, Coops, Roijackers, Buijse, & Scheffer, 2005), followed by other slightly eutrophic species such as *G. densa*, *Hippuris vulgaris*, and *A. repens*. The endangered *G. densa*, for example, originally occurred near Gabčíkovo, in a natural small stream's upper reaches (Ot'ahel'ová & Husák, 1992). After the hydropower plant was activated, the stream dried out and *G. densa* had vanished, but as soon as in 1996 it was repeatedly recorded, this time in a new seepage canal (Ot'ahel'ová, 1998). Similarly, Kohler and Schneider (2003) found *G. densa* and *H. vulgaris* in its greatest density in slightly eutrophic reaches; both, however, were absent in sections with higher nutrient supply in the Moosach river. New Seepage Water-bodies have increased the heterogeneity and biodiversity of the landscape, providing a secondary habitat for endangered and rare species. Many aquatic plant species have found a refuge in these man-made habitats; nevertheless, their occurrence might probably be a temporal phenomenon.

The Slovak reaches of the Danube River corridor is a unique floodplain ecosystem. The relevant part, "Dunajské luhy", is listed in the Ramsar Convention as an internationally important wetland. Twenty-nine endangered species of the Slovak flora were found in this area during our study. Unfortunately, new man-modified aquatic habitats are being successfully invaded by the alien species *E. nuttallii*.

Our results suggest that the connectivity types of river water bodies, primarily characterised by different hydrologic dynamics and human impact expressed in land-use types, are responsible for the variability of aquatic macrophyte assemblages along the Danube corridor in Slovakia. These factors include the complex of disturbance pattern with a wide amplitude of pressure in time and space.

Acknowledgements

The study was supported by the VEGA 5083 Project from the Grant Agency of Slovak Academy of Sciences and Ministry of Education and by the MIDCC project founded by Austrian Federal Ministry of Education, Science, and Culture. We are grateful to Mr. Tibor Kiss for his kind assistance with the field research. We are grateful for constructive suggestions of two anonymous reviewers of this paper.

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