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Effect of environmental variables on the aquatic macrophyte composition pattern in streams: a case study from Slovakia

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With 3 figures and 2 tables

Abstract: The relationships between macrophyte assemblage composition and environmental variables were assessed across 39 Slovak streams in the Pannonicum and Carpathicum bioregions. Twenty-one environmental variables including geographical characteristics, hydrology, physical habitat, water chemistry, and anthropogenic stressors were assessed. A total of 89 macrophyte taxa were identified, of which 26 % and 74 % were bryophytes and vascular plants, respectively. Significant differences were observed between the Pannonicum and the Carpathicum bioregions for all studied environmental variables except the following: stream width, the presence of human-made sediment and the phosphate content. Similarly, the number of species as well as the Mean Mass Total of all plant groups was significantly different between the Pannonicum and the Carpathicum regions except for filamentous algae. Macrophyte composition in Slovak streams was affected by sediment type (5.8 %), followed by shading of shrubs and trees on the banks (3.5 %), water depth (3.0 %), NO_2^- (2.8 %) and water acidity (2.2 %). Bryophytes (such as *Brachythecium rivulare*, *Cratoneuron filicinum*, *Hygrohypnum ochraceum*, *Lophocolea heterophylla*, *Marchantia polymorpha* or *Rhynchostegium riparioides*) and only some vascular plants (such as *Persicaria hydropiper* and *Glyceria notata*) occur on coarser sediment types. In contrast, most vascular plants grew on finer sediment types.

Key words: aquatic plants, species-environment relationship, running water, bioregions.

Introduction

Despite being characterised as dynamic systems, running waters often have geographically unique macrophyte assemblages. The distribution, abundance, structure and diversity of macrophytes are affected by several environmental factors and biological interactions. The relative importance of macrophytes varies according to spatial and temporal scales (Lacoul & Freedman 2006). Some important environmental factors are associated with light requirements of plants (Tremp 2007), sediment characteristics (Schneider & Melzer 2004, Paal et al. 2007), trophic status (Schorer et al. 2000, Kočić et al. 2008) and hydrology (Trémolières et al. 1994, Madsen et al. 2001). Generally, ecological factors influencing species composition in running waters form a set of various physical and chemical properties which can be different in particular countries or regions (Thiébaut & Muller 1999, Riis et al. 2000, Baattrup-Pedersen et al. 2006, Šraj-Kržič et al. 2007). Moreover, anthropogenic influences modify many of the above mentioned characteristics (Ped-

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ersen et al. 2006), including macrophyte distribution patterns.

The relationships between lotic macrophytes and environmental factors have primarily been studied in rivers (Ferreira & Moreira 1999, Bernez et al. 2004). In contrast, there have been fewer such studies in smaller streams (Riis et al. 2000, Downes et al. 2003, Baattrup-Pedersen et al. 2006). This may be due to the successful colonisation and higher survival of macrophytes resulting in higher species diversity in rivers and larger canals compared to smaller streams (Riis et al. 2001, Williams et al. 2003). Furthermore, the higher economical exploitation of larger running waters is also an important consideration. On the basis of macrophyte-environment relationship studies, the ecological classification of macrophytes was performed for several geographical regions in Europe (e.g. Haury et al. 2000, Schaumburg et al. 2004). While many European countries have developed ecological classifications, the characterisation of stream macrophyte-environment relationships is lacking in Slovakia. Recently, a few case studies from Slovak rivers were published (e.g. Hrivnák et al. 2006, Oťaheľová et al. 2007) but these were not based on a country-wide stream coverage. We, therefore, tried to provide a more comprehensive view. Although Slovakia has a relatively small territory, it has various morphological, geological and climatic features which are manifested in the ecological impact on the stream network. The main objective of this study was to evaluate the relationships between macrophyte assemblage composition and environmental conditions in Slovak streams.

Methods

Field sampling

Field research was carried out from July to August 2006 during peak biomass for most species. We selected 39 streams in the Slovakian territory with respect to both geographical and phytogeographical regions both within the Pannonicum and Carpathicum regions. The border between the basic European Alpine and Pannonian biogeographical regions passes through Slovakia and is more or less identical to the Carpathicum and Pannonicum phytogeographical regions (http://ec.europa.eu/environment/nature/natura2000/sites_hab/biogeog_regions). Within each stream, we chose two 100-m-long sections (hereafter referred to as sampling sites) reflecting the gradient of land use and anthropogenic influences. The first was situated in the upper reaches of a stream in a relatively natural environment and the second was much lower in the stream, usually located in the countryside associated with strong human activities. Every sampling site was divided into five contiguous 20-m-long subsections where all macrophytes (bryophytes, vascular plants, and macroscopic algae) were surveyed using a five level scale ("Plant Mass Estimate"; 1 – rare, 2 – occasional, 3 – frequent, 4 – abundant, 5 – very abundant; Kohler & Janauer 1995).

Twenty-one environmental variables were assessed (for details see Table 1). In each subsection of a sampling site, the following variables were evaluated: stream averaged width (Width), averaged water depth (Depth), averaged sediment depth (SedDepth; the three above mentioned variables were measured over the length of the subsection), shading by woody vegetation on banks (Shading), the presence of human-made bank and human-made sediment (ArtBank and ArtSediment), bed material (Sediment) and flow velocity class (Flow velocity). A sampling site was then characterised by the mean of the continuous quantitative variables and the dominant category of the category variables. The remaining variables of the sampling site were evaluated as a whole: the Pannonicum or Carpathicum region (as a binary variable), the shape of the stream-course (Sinuosity), the proportion of natural land cover (wetlands, woody vegetation; NaturalLanduse), altitude (measured by GPS at the central point of a sampling site; Altitude), the distance from the stream source (from map; Stream source), bedrock type (Calcareous and Non-calcareous), climatic district following Lapin et al. (2002; Climate), temperature (WTemperature), pH (WpH) and conductivity (WConductivity) of the water (by pH-meter/conductometer WTW pH/Cond 340i) and chemical water variables. For chemical analysis in the laboratory, water samples were collected from each sampling site, quickly frozen and maintained at –18 °C until the ammonia, nitrite, nitrate and phosphate contents were measured. The ammonia content was determined by an ion-selective electrode at 20 °C; the nitrite content was determined spectrophotometrically at $\lambda = 540$ nm, after diazotisation with 40 g/l sulphanilamide and 2 g/l *N*-(1-naphthyl)-ethylenediamine dihydrochloride in 10 % H_3PO_4. The combined nitrate and nitrite level in the water samples was measured by the same method except that the samples were reduced with 1.4 g/l hydrazinsulphate, 7.5 g/l $CuSO_4$ and then neutralised by adding 3 g/l NaOH prior to the diazotisation (Braun-Systematik, Menthodenblatt N60). The nitrate content was then calculated as the difference in the absorbance of the same sample with and without reduction. If the nitrate content in the sample was above 0.1 mg/l, its level was controlled using an ion-selective electrode at 20 °C. The phosphate content in the samples was analysed spectrophotometrically according to the modified method described by Chen et al. (1956). Briefly, the absorbance of the samples was measured at $\lambda = 720$ nm, after derivatisation with an ammonium-molybdate reagent containing 0.1 M sulphamic acid, 0.01 M ammonium molybdate, 0.1 M potassium antimonyl oxide tartarate and 0.1 M ascorbic acid.

Data analysis

Based on Plant Mass Estimate data, the Mean Mass Total (MMT) of each species in the sampling site was calculated (cf. Kohler & Janauer 1995). Detrended correspondence analysis (DCA) was used for testing the applicability of linear or unimodal ordination methods. The length of gradient was 9.456, indicating that the unimodal model was suitable for the analysis. Rare species were downweighted. The effect of environmental variables on species variability was assessed by employing canonical correspondence analysis (CCA), using the CANOCO 4.5 for Windows package (ter Braak & Šmilauer 2002). Of the 78 sites sampled, two sites were excluded from the surveys and

Table 1. Survey of environmental and selected species variables of Slovak streams (means and standard deviations are given for continuous variables, relative proportions of the dominant category for category variables, and percentage for the binary variable).

Variable	Pannonicum region	Carpathicum region	Total	P-value
Number of sampling sites	30	46	76	
Species variables				
Number_species	5.3 (3.6)	3.4 (2.7)	4.2 (3.2)	*
Sum_MMT_Algae	0.8 (1.4)	1.3 (1.6)	1.1 (1.5)	ns
Sum_MMT_Mosses	0.4 (0.8)	2.1 (2.9)	1.4 (2.5)	***
Sum_MMT_Vascular	6.9 (5.7)	1.2 (3.3)	3.4 (5.2)	***
Sum_MMT	8.1 (5.8)	4.6 (4.4)	6.0 (5.2)	**
Measured or estimated environmental variables				
Alt (m)	179.3 (59.9)	427.5 (168.1)	329.5 (182.4)	***
Stream source (km)	20.1 (12.9)	10.7 (7.4)	14.4 (10.87)	**
Width (m)	4.1 (3.4)	4.0 (2.9)	4.1 (3.1)	ns
Depth (cm)	42.1 (34.4)	23.3 (10.7)	30.6 (24.6)	*
Sed Depth (cm)	8.3 (13.3)	1.4 (3.1)	4.1 (9.3)	***
Shading (%)	27.8 (37.1)	57.4 (33.0)	45.7 (37.4)	**
Natural Landuse (%)	26.6 (39.7)	48.5 (42.6)	39.8 (42.6)	*
Art Bank (%)	73.1 (44.7)	24.7 (40.7)	43.8 (48.3)	***
Art Sediment	9.3 (23.3)	3.1 (9.2)	5.5 (16.4)	ns
W Temperature (°C)	21.1 (4.3)	15.0 (3.0)	17.4 (4.7)	***
W pH	8.1 (0.4)	8.3 (0.5)	8.2 (0.5)	*
W Conductivity (μS/cm)	473.4 (247.9)	267.7 (155.8)	348.9 (220.4)	***
NH_4^+ (mg/l)	1.2 (3.7)	0.1 (0.09)	0.5 (2.4)	***
NO_3^- (mg/l)	1.3 (1.5)	1.6 (1.7)	1.5 (1.6)	*
NO_2^- (mg/l)	0.7 (2.1)	0.1 (0.07)	0.3 (1.3)	*
PO_4^{3-} (mg/l)	0.6 (1.3)	0.1 (0.2)	0.3 (0.9)	ns
Category environmental variables (dominant category in %)				
Sediment	4 (50)	2 (63)	2 (49)	
Flow velocity	1 (57)	2 (65)	2 (57)	
Sinuosity	1 (37)	2 (37)	2 (36)	
Climate	12 (23)	2 (24)	2 (14), 7 (14)	
Binary environmental variables (%)				
Calcareous rocks	43	52	49	

The assessed variables were compared between the Pannonicum and Carpathicum regions using the Mann-Whitney *U*-test (ns = non-significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Explanations of category variables: Sediment (1 = rock and large artificial material, 2 = gravel, 3 = sand, 4 = fine substrate); Flow velocity (1 = 0–30 cm/s, 2 = 35–65 cm/s, 3 > 70 cm/s); Sinuosity (1 = absolute straight channel, 2 = straight channel, 3 = slightly sinuous channel, 4 = moderately sinuous channel, 5 = meandering channel); Climate (1 = cool mountainous, 2 = moderately cool, 3 = moderately warm and very humid, 4 = moderately warm and humid-highlands, 5 = moderately warm and humid-basins, 6 = moderately warm and humid-planes, 7 = moderately warm and moderately humid-highlands, 8 = moderately warm and moderately humid-hilly lands, 9 = warm and moderately humid with cool winter, 10 = warm and moderately humid with mild winter, 11 = warm and moderately dry with cool winter, 12 = warm and moderately dry with mild winter, 13 = warm and dry with cool winter, 14 = warm and dry with mild winter, 15 = warm and very dry). For further explanations see Methods.

analyses because they contained no macrophytes and another two sites were excluded from the ordinations because they were outliers in the DCA analysis. The significance of the environmental variables was tested by the Monte Carlo permutation test (9999 runs). Moreover, the environmental variables were compared between the Pannonicum and Carpathicum regions using the Mann-Whitney *U*-test. The relationships between the environmental and species variables were assessed by Spearman's rank correlation coefficient using the STATISTICA software (Statsoft 2001).

Nomenclature

The names of bryophytes and vascular plants are presented according to Marhold & Hindák (1998). Although most bryophytes were identified at the species level, we pooled the bryophytes that we were unable to identify (8 specimens) into Marchantiophyta or Bryophyta. Similarly, we did not characterise the taxonomy of macroscopic filamentous algae (Charophyceae were not found), therefore these were treated collectively as filamentous algae.

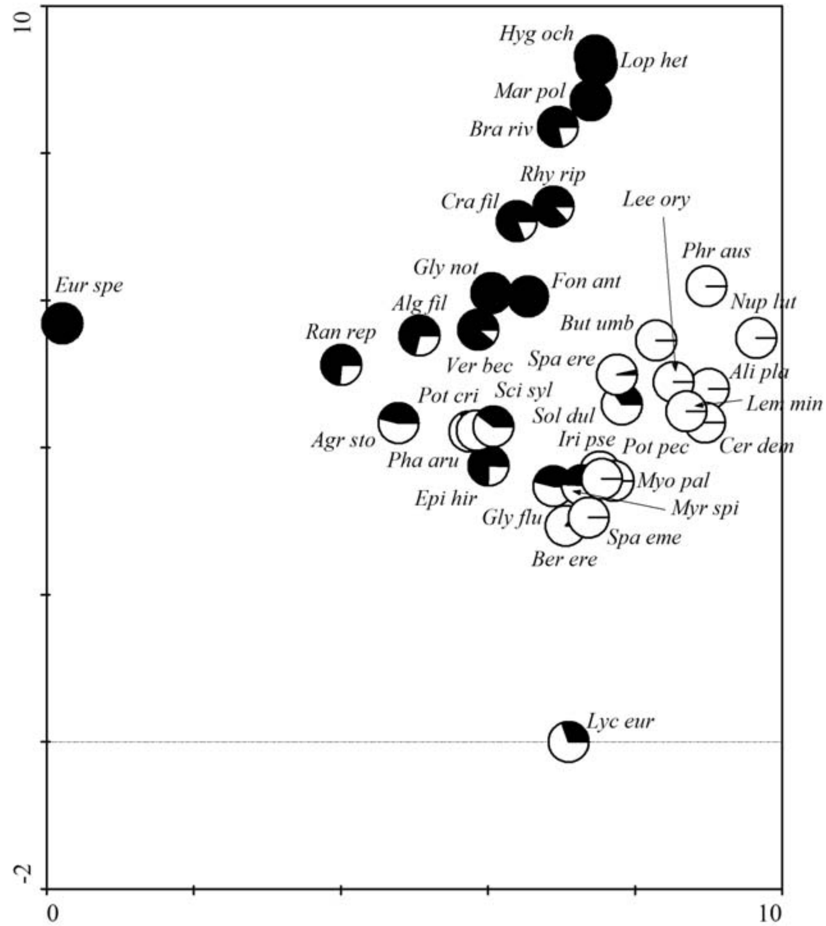

Fig. 1. Detrended correspondence analysis (first two axes explain 14.7 % of the variance in the species data), pie symbols plot the visualising distribution of species over classes with different ratios of the Pannonicum/Carpathicum regions category (black – Carpathicum, white – Pannonicum). Only species occurring in at least at three sampling sites are shown (Marchantiophyta and Bryophyta were excluded). Abbreviations of the species are explained in Fig. 2.

Results

We found 89 macrophyte taxa (including the three broad groups of filamentous algae, Marchantiophyta and Bryophyta) in the sampling sites of Slovak streams; almost 26 % of these taxa belong to the Bryophytes and more than 74 % to the vascular plants. Mainly Bryophytes (such as *Hygrohypnum ochraceum*, *Lophocolea heterophylla* and *Marchantia polymorpha*) and only a few of the vascular plants (such as *Glyceria notata* and *Petasites hybridus*) were recorded in the Carpathicum region. In contrast, sites in the Pannonicum region were represented by many vascular plants, including typical aquatic plants (such as *Ceratophyllum demersum*, *Nuphar lutea* and *Potamogeton pectinatus*), amphiphytes (such as *Butomus umbellatus* and *Sparganium emersum*) and helophytes (such as *Iris pseudacorus* and *Leerzia oryzoides*). Some of the species, such as *Agrostis stolonifera*, *Glyceria fluitans* and *Myriophyllum spicatum*, occurred in both phytogeographical regions (Fig. 1). The mean number of species per sampling site was relatively low (4.2; range 1–15 species), but in the Pannonicum region, this value was significantly higher ($P < 0.001$). Except for filamentous algae, the MMT of all plant groups was significantly ($P < 0.01$) different between both regions (Table 1). Strong and highly significant ($P < 0.001$) correlations were found between the Sum of MMT of all species (SumMMT) and the Number of species ($r_s = 0.91$), the SumMMT and the Sum of MMT of vascular plants (SumMMTVascular; $r_s = 0.75$) and the SumMMTVascular and the Number of species ($r_s = 0.72$).

Significant differences ($P < 0.05$) between the Pannonicum and the Carpathicum regions were found for all but three environmental variables (Table 1). Among the category variables, coarser sediment types, higher flow velocity and sinuosity as well as cooler climate and higher precipitations were typical for the Carpathicum region compared to the Pannonicum region (Table 1). The highest and highly significant ($P < 0.001$) correlations were calculated for the following pairs of environmental variables: Temperature of water and Altitude ($r_s = –0.80$), Shading and Artificial

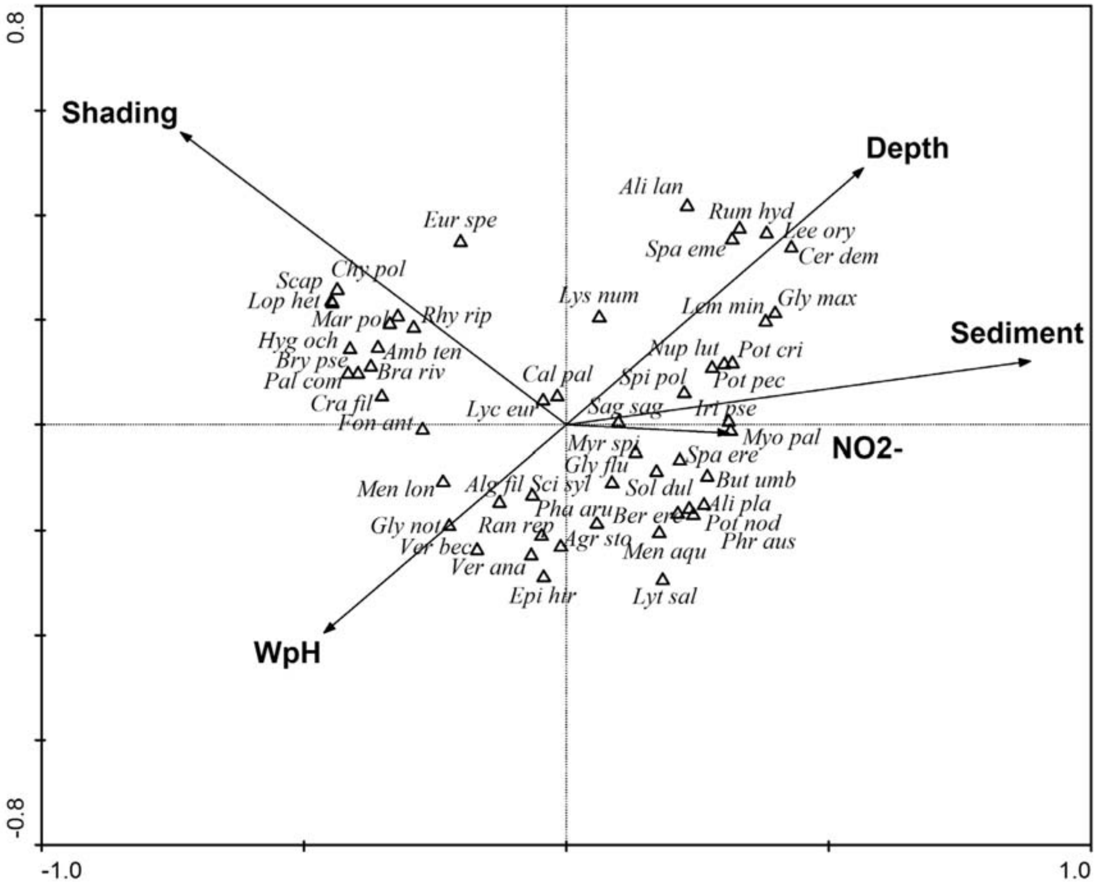

Fig. 2. Canonical correspondence analysis, species position and significant environmental variables. Only species occurring in at least at two sampling sites are shown (Marchantiophyta and Bryophyta were excluded). The first two axes explained 10.5 % variance of the species data and 61.1 % variance of the species-environment relationship. Abbreviations of species: Agr sto = *Agrostis stolonifera*, Alg fil = filamentous algae, Ali lan = *Alisma lanceolatum*, Ali pla = *Alisma plantago-aquatica*, Amb ten = *Amblystegium tenax*, Ber ere = *Berula erecta*, Bra riv = *Brachythecium rivulare*, Bry pse = *Bryum pseudotriquetrum*, But umb = *Butomus umbellatus*, Cal pal = *Caltha palustris*, Cer dem = *Ceratophyllum demersum*, Chy pol = *Chiloscyphus polyanthos*, Cra fil = *Cratoneuron filicinum*, Epi hir = *Epilobium hirsutum*, Eur spe = *Eurhynchium speciosum*, Fon ant = *Fontinalis antipyretica*, Gly flu = *Glyceria fluitans*, Gly max = *Glyceria maxima*, Gly not = *Glyceria notata*, Hyg och = *Hygrohypnum ochraceum*, Iri pse = *Iris pseudacorus*, Lee ory = *Leerzia oryzoides*, Lem min = *Lemna minor*, Lop het = *Lophocolea heterophylla*, Lyc eur = *Lycopus europaeus*, Lys num = *Lysimacia nummularia*, Lyt sal = *Lythrum salicaria*, Mar pol = *Marchantia polymorpha*, Men aqu = *Mentha aquatica*, Men lon = *Mentha longifolia*, Myo pal = *Myosotis palustris* agg., Myr spi = *Myriophyllum spicatum*, Nup lut = *Nuphar lutea*, Pal com = *Palustriella commutata*, Pha aru = *Phalaroides arundinacea*, Phr aus = *Phragmites australis*, Pot cri = *Potamogeton crispus*, Pot nod = *Potamogeton nodosus*, Pot pec = *Potamogeton pectinatus*, Ran rep = *Ranunculus repens*, Rhy rip = *Rhynchostegium riparioides*, Rum hyd = *Rumex hydrolapathum*, Sag sag = *Sagittaria sagittifolia*, Scap = *Scapania* sp., Sci syl = *Scirpus sylvaticus*, Sol dul = *Solanum dulcamara*, Spa eme = *Sparganium emersum*, Spa ere = *Sparganium erectum*, Spi pol = *Spirodela polyrhiza*, Ver ana = *Veronica anagallis-aquatica*, Ver bec = *Veronica beccabunga*

bank (ArtBank; r_s = –0.78), Natural land cover (NaturalLanduse) and ArtBank (r_s = –0.72), Temperature of water and Ammonia content (r_s = 0.72), Shading and NaturalLanduse (r_s = 0.66) and Shading and Stream source (r_s = –0.66). Considering the species variables, SumMMTVascular strongly correlated with Shading (r_s = –0.70) and ArtBank (r_s = 0.65).

The first two axes of the CCA explain 10.5 % of the variance of the species data and 61.1 % of the variance of the species-environment relationship. Along the first axis, the species are arranged from habitats with coarser sediment type, more shaded, with shallower water and with lower nitrite content (mainly bryophytes) to species growing on fine sediment type, in deeper and more open water with a higher nitrite content (mainly true aquatic plants, amphiphytes and some helophytes; Fig. 2). According to the results of forward selection in CCA, the macrophyte composition was affected by Sediment (5.8 %), followed by Shading (3.5 %), Depth (3.0 %), NO_2^- (2.8 %) and WpH (2.2 %). These five

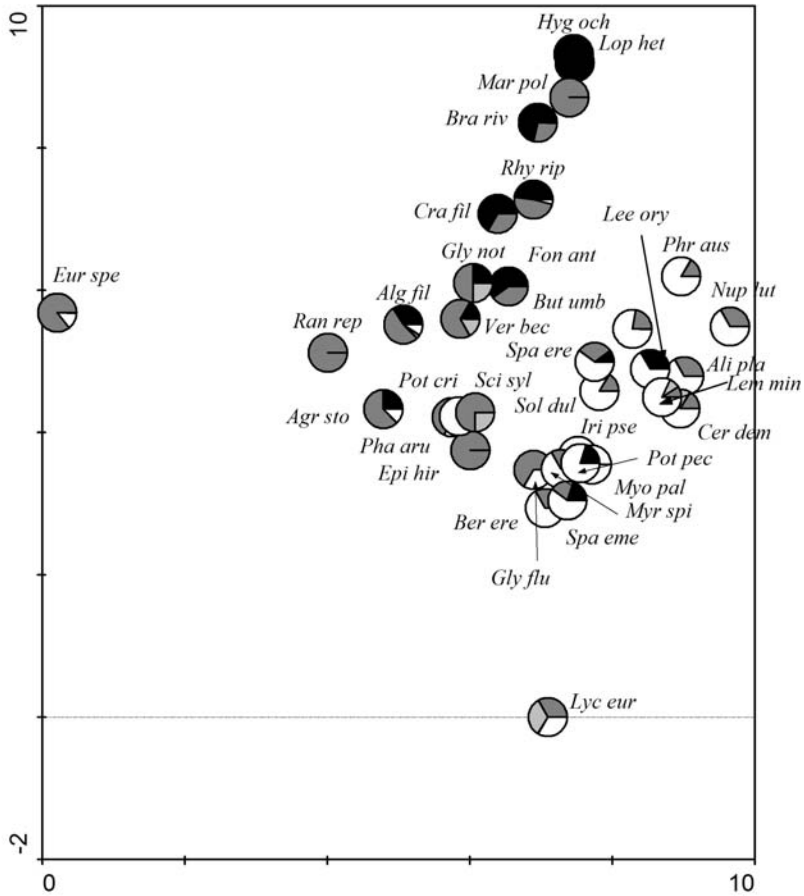

Fig. 3. Detrended correspondence analysis (the first two axes explain 14.7 % variance of the species data), pie symbols plot the visualising distribution of species over classes with different proportions of the sediment category (black – rock and large artificial material, grey – gravel, lighter grey – sand, white – fine substrate). Only species occurring in at least at three sampling sites are shown (Marchantiophyta and Bryophyta were excluded). Abbreviations of the species are explained in Fig. 2.

significant ($P < 0.05$) variables explain 17.3 % of the total variance. Seven environmental variables had a significant effect and the highest values had Depth and Nitrite content (both 2.4 %; Table 2). The relation of species to the most significant environmental variables (Sediment) is illustrated in Fig. 3. Bryophytes (such as *Cratoneuron filicinum*, *Hygrohypnum ochraceum* and *Lophocolea heterophylla*) and some vascular plants (like *Persicaria hydropiper* and *Glyceria notata*) occur on coarser sediment types. On the other hand, most vascular plants grew on finer sediment types.

Discussion

Differences between phytogeographical regions as environmental variables and macrophyte pattern

Both phytogeographical regions are determined by different ecological conditions which are reflected in different floristic compositions. This fact was confirmed also by our study. Significant differences were found for the majority of environmental factors as well as for the total number of species or mean mass total (Table 1). On average, lower altitudes, higher average air temperatures, and remarkably higher influence of anthropogenic characteristics were found in the Pannonicum region. Additional characteristics included predominating fine sediments, slower velocity of water and higher water temperatures, depth and conductivity of water or presence of the majority of chemical compounds (Table 1). As expected, numerous environmental differences were closely related to the geographical location (latitude and altitude), climatic features (e.g. water temperature) and hydrological and geomorphological features (e.g. sinuosity, flow velocity, depth of water). Other differences (e.g. Shading, NaturalLanduse, "artificial" character or chemical characteristics) are associated with a higher intensity of landuse in the lowlands, typical for the Pannonicum region. Some of the differences were predictable, but the amounts of nitrate in water were unexpected. The relatively high average values and range of nitrate content detected in the Carpathicum region (Table 1) confirm that the environment in all parts of Slovakia is still under strong nitrate pollution (caused by agricultural activities and

Table 2. Canonical correspondence analysis: results of forward selection (marginal effect = percentage variance explained by an individual variable while used as the only constraining variable; conditional effect = additional variance explained by the variable at the time it was included in the stepwise selection; pure effect = percentage variance explained by the variable after all variables that are significant when alone were used as covariables). Variance explained is shown as a percentage of total inertia. ns – non-significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Environmental variable	Effect		
	Marginal	Conditional	Pure
Sediment	5.8***	5.8***(1)	1.7*
Alt	5.6***	.	1.5 ns
Pannonicum	5.6***	.	1.3 ns
Art Bank	5.6***	.	1.1 ns
Climate	5.6***	.	1.2 ns
W Temperature	5.3***	.	1.4 ns
Shading	5.3***	3.5***(2)	1.7*
Flow velocity	5.2***	.	1.2 ns
Depth	4.2***	3.0***(3)	2.4**
Sinuosity	4.0***	.	1.7*
Natural Landuse	3.9***	.	2.3 ns
Stream source	3.9***	.	1.7*
W Conductivity	3.4***	.	1.6 ns
W pH	3.4***	2.2*(5)	2.1**
Sed Depth	3.3*	.	2.0 ns
NO_2^-	2.9*	2.8*(4)	2.4*
PO_4^{3-}	2.4 ns	.	.
Calcareous rocks	2.2**	.	1.4 ns
NH_4^+	2.0 ns	.	.
Width	1.8 ns	.	.
Art Sediment	1.8 ns	.	.
NO_3^-	1.7 ns	.	.
Explained variance by all variables (%)	43.0	.	.
Explained variance by significance variables (%)	.	17.3	.

urban sources; cf. Majer et al. 2005). In the Pannonicum region (mainly characterised by bigger lowland streams), the species diversity was significantly higher, with remarkable predominance of vascular plants (true aquatic species and helophytes). For the streams in the Carpathicum region (mainly smaller mountain streams), mostly non-vascular plants and only a small number of vascular plants (such as *Glyceria notata*, *Petasites hybridus* and *Veronica beccabunga*) were typical (Table 1, Fig. 1). A similar pattern of increasing plant diversity from small mountain streams with bryophytes towards bigger lowland streams with rich vascular plants was found in the all regions of Europe (Baattrup-Pedersen et al. 2006). The presence of liverworts, mosses or lichens in streams probably indicate that a site is unimpacted by hydro-morphological degradation (O'Hare et al. 2006). The different environmental conditions, together with the variability in the plant species composition in various biogeographic regions, resulted in the determination of specific evaluation criteria and ecological classification of water organisms by the European Water Framework Directive (Schaumburg et al. 2004, Krno et al. 2007).

Species-environment relationship

Among the environmental characteristics satisfying the forward selection in the CCA, five showed a significant effect on macrophyte species composition – type of sediment, shading by shrub and tree vegetation on banks, water depth, water pH and nitrite content in water.

The substrate parameter (sediment) was the most important environmental factor in determining macrophyte distribution in Slovak streams. It explained almost 6 % of the species data variability (Table 2). Sediment size and sediment accumulation belong to the factors considerably influencing species distribution, abundance and diversity of macrophytes in running waters (Baattrup-Pedersen & Riis 1999, Ferreira & Moreira 1999, Kuhar et al. 2007). Several macrophytes occurred exclusively on coarser sediments. In our study, we detected this preference mainly for bryophyte species (*Brachythecium rivulare*, *Cratoneron filicinum*, *Fontinalis antipyretica*, *Hygrohypnum ochraceum*, *Lophocolea heterophylla*, *Marchantia polymorpha*, *Rhynchostegium riparioides*). The fact that substrate texture is often a key predictor of bryophyte presence, cover and species number was confirmed by several studies (Suren 1996, Downes et al. 2003, O'Hare et al. 2006). Bryophytes prefer coarser sediments, stones or blocks of rocks (Downes et al. 2003). The stability of these sediment types within the dynamic stream hydrology regime is a prerequisite for the long-term presence of bryophytes. On the other hand, our findings show that finer sediment is mainly preferred by typical aquatic species (*Ceratophyllum demersum*, *Myriophyllum spicatum*, *Nuphar lutea* and *Potamogeton crispus*) as well as some amphiphyte and helophyte species (such as *Alisma plantago-aquatica*, *Butomus umbellatus* and *Iris pseudacorus*). However, helophytes grew from the coarsest to the finest or organic sediment types (see Fig. 3). Our findings were mirrored by Willby et al. (2000) who classified *Ceratophyllum demersum*, *Lemna minor*, *Nuphar lutea* to species growing on fine (silt and clay) and medium (sand) type of substrate. Some other species, such as *Myriophyllum spicatum* or *Potamogeton crispus* are considered to be species with a wider range of substrate types. Similarly, other studies focused on running water referred to the previously mentioned species as growing on various sediment types (Clarke & Wharton 2001, Hrivnák et al. 2006).

Light availability is a critical factor in photosynthesis and is limiting the distribution of aquatic plants (Lacoul & Freedman 2006). Forests and shrubs on banks of streams reduce light amount on/under the water surface. Given that the mean width of our studied streams is approx. 4 m (see Table 2), shading caused by woody riparian growths play a conspicuous role. In our study, the shading proved to be the second most important factor affecting the species composition in streams (Table 2). Higher shading favours bryophytes but amphiphytes, typical helophytes and true aquatic plants favour mainly open habitats with minimum shading (Fig. 2). A significant influence of shading on the vegetation of running waters is in accordance with the results of for example Tremp (2007).

Water depth has the highest pure effect on macrophyte composition (Table 2). This parameter is closely related to other factors, such as water transparency or turbidity, associated with light availability for macrophytes. Water depth is considered a very important physical factor by several authors (Bernez et al. 2004, Daniel et al. 2006). Mainly Bryophytes but some spring helophytes (e.g. *Glyceria notata* or *Veronica beccabunga*) were also found in shallow waters typical of mountain rivulets and streams. However, vascular plants were common in medium-deep or deep streams (Fig. 2). In a study of European streams without human impact, Baattrup-Pedersen et al. (2006) found a very similar pattern, namely a shift from the predominance of species-poor, moss- and liverwort-dominated communities in small-sized, shallow mountain streams to more rich communities dominated by vascular plants in the medium-sized, lowland streams.

A significant influence on macrophyte species composition was also detected for two chemical characteristics – pH and nitrite content in water (Table 2 and Fig. 2). Water reaction (pH) measured on study plots displayed only minimal variability within a range of neutral to slightly alkaline. A majority of streams consist of water with alkaline pH (Table 1). In spite of this, pH seems to be an important factor for the distribution pattern of macrophytes in Slovak streams (Table 2). Moreover, the influence of pH is more significant for lentic ecosystems (cf. Lacoul & Freedman 2006) but it can be important for explaining both species distribution and the abundance pattern of macrophytes in running waters (Ferreira & Moreira 1999, Thiébaut & Muller 1999, Dodkins et al. 2005, Kočić et al. 2008). On smaller scales (e.g. within one river with uniform geological substrate), pH becomes unimportant because its variation is negligible (Hrivnák et al. 2006). Among the selected nitrogen characteristics (ammonium, nitrate and nitrite content), only nitrite content had a significant effect (Table 2). Measured values of nitrite in Slovak streams within the Carpathicum region are relatively low. Similar or lower nitrite contents in water are typical for most European streams (Bernez et al. 2004, Trei & Pall 2004, Dodkins et al. 2005). In contrast, substantially higher values were detected in streams of the Pannonicum region (Table 1). This fact can be explained by the strong pollution of lowland streams in southern Slovakia due to human activities such as agricultural activity, leaking sewage lines, septic systems and compost piles. Phosphate and nitrogen are the main elements limiting plant productivity and growth although other nutrients may also play an important role in the composition of macrophyte vegetation in running water bodies (Schneider & Melzer 2004, Lacoul & Freedman 2006, Kočić et al. 2008). Nitrogen in various chemical forms is commonly considered the most indicative ecological characteristics for the assessment of water quality and classification based on aquatic plants by the Water Framework Directive of the European Community (Schaumburg et al. 2004, Haury et al. 2006).

The percentage of the explained variability by the studied environmental variables within conditional effect in CCA was relatively low. It indicates a necessity of including additional environmental variables that are expected to be relevant for the distribution and composition of macrophytes in streams. Among them, some sediment characteristics (e.g. accumulation, stability, heterogenity, trophic status, content of nutrients and some other chemical parameters) or hydrological characteristics (e.g. flood disturbance, water level fluctuation during the year) are very important (Baattrup-Pedersen & Riis 1999, Downes et al. 2003, Lacoul & Freeman 2006, Šraj-Kržič et al. 2007). Overall, our results provide a basis on which to define the reference conditions for assessing the ecological status of streams according the Water Framework Directive of the European Community. Interestingly, the differences detected in both environmental and species characteristics between the two phytogeographical regions showed that an independent evaluation of macrophytes is required.

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