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Seasonal dynamics of macrophyte abundance in two regulated streams

Research Article

Richard Hrivnák[1,*], Helena Oťaheľová[1], Dušan Gömöry[2]

[1]*Institute of Botany, Slovak Academy of Sciences, SK-845 23 Bratislava, Slovakia*

[2]*Department of Phytology, Faculty of Forestry, Technical University in Zvolen, SK-960 53 Zvolen, Slovakia*

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Abstract: This study analysed seasonal dynamics of macrophyte abundance in two perennial lowland regulated streams (Stream 1 and 2) in the Danube basin (Slovakia). Assessments of macrophyte abundance and environmental characteristics were accomplished 7 times during the vegetation period in 2005 within a 100 m long section. Statistically significant differences in total abundance of macrophytes as well as an abundance of macrophyte groups (hydrophytes, amphiphytes, helophytes) and *Potamogeton nodosus* were detected among months within the vegetation period. Abundance fluctuations for individual macrophyte groups and species were moderate in Stream 1 and much stronger in Stream 2. Only amphiphytes showed bimodal temporal distribution in Stream 1, but the abundance of this group was low, reflecting more or less random occurrence of species in vegetation period. Multiple linear regression revealed that water depths and air temperature are the most significant environmental variables affecting the seasonal pattern of total as well as dominating group abundance in Stream 1 and 2, respectively. In all cases, abundances are significantly influenced by the abundance of the respective group in the preceding month. Culmination time differed between streams for all macrophyte groups except helophytes. Total abundance culminated 0.57 month later in the Stream 1 compared to Stream 2.

Keywords: *Aquatic plants • Central Europe • Positive feedback • Relative plant quantity • Running water*

1. Introduction

Macrophytes are defined as true aquatic and amphibious plants including macroscopic algae, bryophytes and vascular plants [1]. Their distribution and abundance are affected by several environmental and artificial factors and their interactions [2]. There are several main groups of influences to macrophytes in running waters: climate, hydrology, geomorphology, nutrients and other chemical factors, biological interactions and human activities [e.g. 3-10]. The flow regime of a stream is one of the major factors directly or indirectly controlling the biota, including vegetation [11]. The listed factors affect not only the interannual but also the seasonal dynamics of macrophytes. Seasonal fluctuations are affected primarily by the changes of climatic characteristics and the related changes in hydrology: the maximum development of macrophytes is observed at the beginning of the second half of the vegetation season, which equates to the summer months in Central Europe. When both air and water temperatures rise and the day-length becomes longer in spring, production of macrophytes increases. On the other hand, lower temperatures and the shortening of day-length in the autumn cause a decreasing macrophyte production [12-14].

Most studies of seasonal dynamics of macrophytes focused on water flows with relatively stable water regimes [e.g. 12,14,15], just to eliminate the effect of fluctuations. For our study, two streams with different water-level fluctuation regimes were chosen and we focused on the following questions: 1) What is the temporal course of the macrophyte abundance in lowland streams? 2) Are the seasonal dynamics different for different groups of aquatic plants? 3) Which of the environmental factors that we studied explain best the seasonal dynamics of abundance of aquatic plants?

* *E-mail: richard.hrivnak@savba.sk*

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2. Experimental Procedures

Two perennial lowland regulated streams in the Danube basin were selected for this study:

1) The stream near the Kúty village in the Morava river catchment area in southwestern Slovakia (further on, "Stream 1"; geographical coordinates – 48º 39' 34,2" N, 16º 58' 41,7" E; altitude – 152.8 m). Straight stream is canalized with almost vertical banks slope; width of stream is 6 m; the flat plane bed has low depth variation, bed substrate is sand; surrounding biotopes are wetlands and agricultural areas. Stream is slightly shaded by trees, moderately eutrophic; conductivity of water is 713 μS.cm^{-1} and pH 8.05–8.09 (measured at the end of April 2005).

2) Tuhársky potok stream at the margin of the Lučenec town in the Ipeľ river catchment area in the southern part of central Slovakia ("Stream 2"; 48º 19' 30,9" N, 19º 40' 42,7" E, altitude –180 m); Sligtly sinuous stream, the left bank side is gradually decreasing whereas the right bank is almost vertical; width of the stream is 5 to 6 m; slightly uneven bottom with gravel, sand and mud as a substrate types; surrounding biotopes are agricultural and urban industrial areas. Stream is slightly shaded by trees, eutrophic; with the conductivity of water of 220 μS.cm^{-1} and pH 8.5–8.6 (measured at the beginning of May 2005).

Both lowland streams are regulated and have more or less similar macro-climatic characteristics, but they exhibit very different water-level fluctuation patterns during the vegetation period. Both sites belong to the warm climatic region, are moderately dry and have a dry subregion with similar mean annual air temperatures (9–10°C and 8–9°C, respectively) and mean annual precipitation totals (500–550 mm and 550–600 mm, respectively), and almost equal mean July air temperatures and precipitation totals (19–20°C and <60 mm, respectively). Both sites had the same air and water temperatures at the beginning of our research (beginning of May 2005) and a similar temporal course of environmental characteristics during the vegetation period, with slightly different absolute values (Figure 1A,B). Similar values were measured for water depth and flow velocity at the beginning of our research in both streams, but their later courses were very different (Figure 1C,D). Due to different stream cross-sections, many smaller and larger spots without any surface water were formed in the Stream 2 during the summer, which were not observed in the Stream 1.

Twenty-six and thirty-four macrophyte plant species were detected in the Stream 1 and 2, respectively. About one third of species were common for both streams.

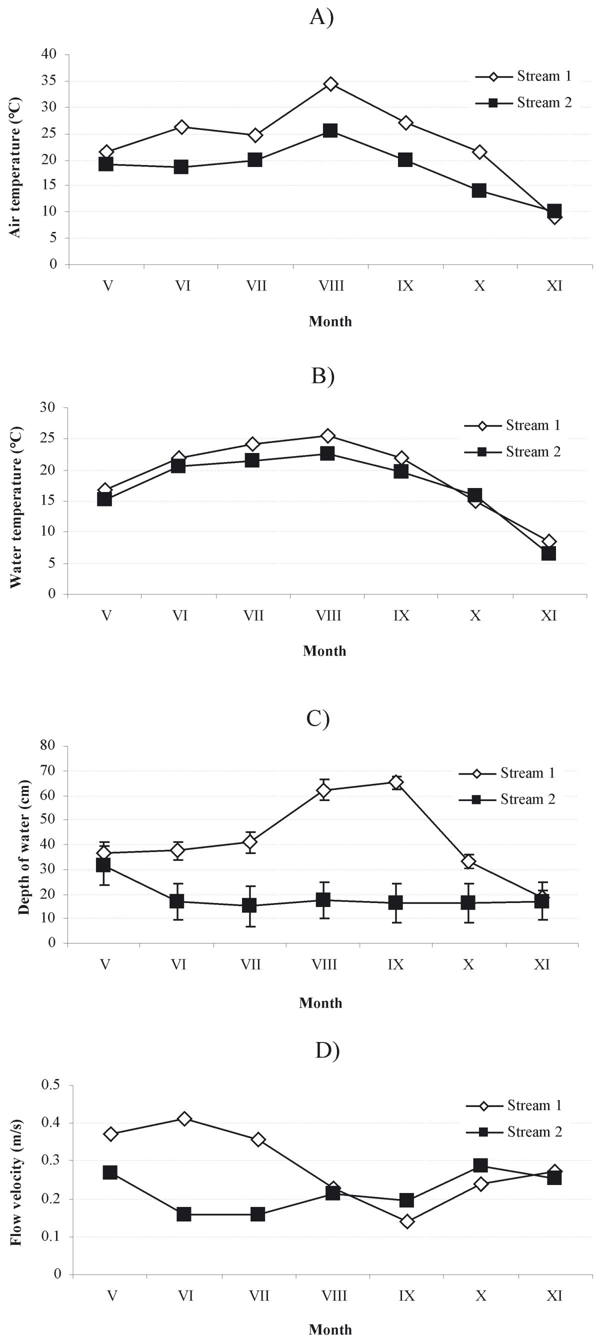

Figure 1. Dynamics of selected environmental characteristics during vegetation period of 2005 for both streams. Air (A, upper) and water (B) temperature, depth (C; mean ± standard deviation) and flow velocity (D, below; mean) of water. Data were recorded at the beginning of the respective month (horizontal axis; from V –May to XI – November).

The most abundant macrophytes were *Sparganium emersum*, *Glyceria maxima*, *Lemna minor* for Stream 1 and *Sparganium erectum*, *Phalaroides arundinacea*, *Potamogeton nodosus* for Stream 2. Mean values of abundance (see below for details) during the vegetation

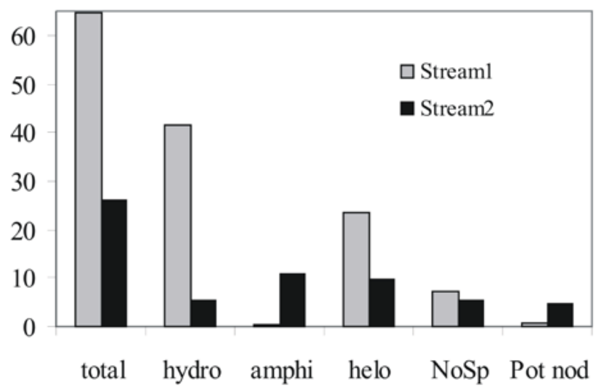

Figure 2. Comparison of mean abundance of aquatic plants during vegetation period of 2005 for both streams. Total – all aquatic plants, hydro – hydrophytes, amphi – amphiphytes, helo – helophytes, Pot nod – *Potamogeton nodosus* and NoSp – number of species.

period are presented in Figure 2. Hydrophytes and amphiphytes were dominant types of macrophytes in Stream 1 and 2, respectively.

Within both streams, 100 m long section was chosen and divided into 10 equally long subsections. Assessments of macrophyte abundance and environmental characteristics were accomplished 7 times during the vegetation period in 2005: at the beginning of May, and subsequently once per month until November. Within each subsection, Plant Mass Estimate (PME) was assessed for all macrophyte species which were classified into three groups (hydrophytes, amphiphytes as well as helophytes growing in aquatic environment of streams; not in the banks) using a five-level scale (1 – rare, 2 – occasional, 3 – frequent, 4 – abundant, 5 – very abundant) [see 16-19 for details]. Air and water temperatures were measured within section once per day at 11:00 a. m., depth of water was measured 10 times per day per subsection at randomly selected places, and flow velocity 3 times per day per subsection.

PME data were transformed into "plant quantity" expressed by relative values (abundance here onwards) using the function $y = x^3$ (y – "plant quantity", x – PME) [17]. "Plant quantity" expresses the relationship between the Plant Mass Estimate data and the true quantity of macrophytes. These transformed values were used in all statistical analyses as a measure of the abundance of the respective macrophyte group or species. Three basic macrophyte groups (hydrophytes, amphiphytes and helophytes), and one macrophyte species, *Potamogeton nodosus*, were evaluated. *Potamogeton nodosus* was chosen for the following reasons: 1) hydrophytes represent the most abundant macrophyte group within the studied streams (summary abundance of this group was the highest), and 2) this hydrophyte species was the only one occurring in both streams.

As the sampled data were potentially spatially as well as temporally autocorrelated, we tested first-order autocorrelations (Pearson's correlation coefficients) for abundance data of macrophyte plant groups.

Differences in abundance among months were tested using one-way analysis of variance.

To assess the relationships between the abundance of individual macrophyte groups and/or species richness and environmental variables, we used multiple linear regression with stepwise selection of variables. As the data were generally temporally autocorrelated, we used an autoregressive model where the respective variable value of the preceding month was included as a predictor.

The temporal distribution of the abundances of most groups over the monitored period was generally unimodal (except amphiphytes in Stream 1 with bimodal distribution of abundance). To assess the time of peak abundance, we fitted the time-abundance curve to the Gaussian function using the multivariate secant method. The estimated means and their asymptotic standard errors were subsequently used for a pairwise comparison between streams using the *t*-test. The package SAS (procedures CORR, REG and NLIN) were used for calculations [20].

3. Results

3.1 Seasonal changes of macrophyte abundance

In addition to amphiphytes and helophytes in Stream 2, there were statistically significant differences (f-test, $P<0.05$) in the abundance of macrophytes among months within vegetation period in the studied streams (Figure 3).

Stream 1: With the exception of amphiphytes, the peak of abundance for all studied macrophyte groups, including *Potamogeton nodosus* and number of species, was observed at the beginning of September (Figure 3). Amphiphytes showed bimodal temporal distribution, but the abundance of this group was generally low, reflecting more or less random occurrence of the respective species during the studied season (Figure 3C). *Potamogeton nodosus* exhibited stable low abundance during the whole vegetation period except a sudden increase at the beginning of September (Figure 3E). Except for the abundance of amphiphytes and the number of species, temporal trends of abundance values are quite consistent (Figure 3). The fluctuation of abundance was moderate and the peak

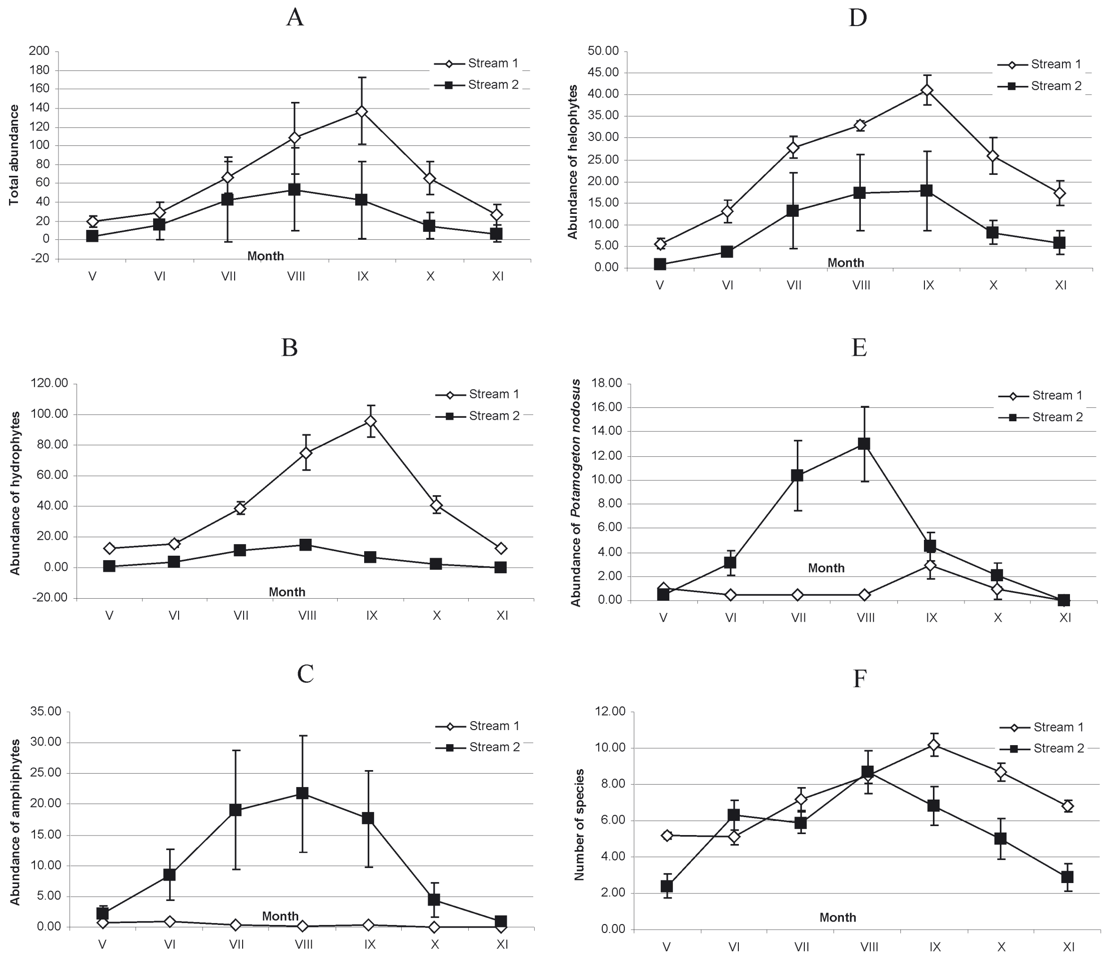

Figure 3. Mean abundance (± standard error) of all aquatic plants during vegetation period of 2005 for both streams. Total – A, hydrophytes – B, amphiphytes – C, helophytes – D, *Potamogeton nodosus* – E and number of species – F. Data were recorded at the beginning of the respective month (horizontal axis).

abundance of hydrophytes exceeded 7.5 times the initial value. For total abundance and helophytes abundance, these differences were similar (a ratio of 7.1 and 7.3, respectively).

Stream 2: Except for helophytes having peak abundance at the beginning of September, all plant groups culminated at the beginning of August (Figure 3). Helophytes exhibited the most stable seasonal course of abundance (Figure 3D). In contrast to the other plant variables, temporal distribution of the number of species was bimodal during the studied vegetation season (Figure 3F). Abundance fluctuations were much more pronounced compared to Stream 1, the peak abundance was 10 times higher than the initial value in the case of total macrophyte abundance, whereby this ratio reached even 29.6 (a ratio of 148 when comparing the peak and the lowest abundance) for hydrophytes, 9.7 for amphiphytes, 19.3 for helophytes and 26.0 for *Potamogeton nodosus*.

3.2 Effect of environmental variables

Multiple linear regression revealed different environmental variables affecting the seasonal pattern of macrophyte abundance (Table 1).

Stream 1: Seasonal dynamics of total abundance as well as the dominating hydrophyte group is influenced by water depth. Total number of species and the abundance of helophytes as the second most frequent group were shown to be significantly affected by water temperature of the preceding month. In all these cases, abundances are significantly influenced by the abundance of the respective group in the preceding month (R^2 ranging from 0.51 to 0.79, see Table 1). For amphiphytes and *Potamogeton nodosus*, regression models showed a very low fit (R^2 = 0.19 and 0.20, respectively).

Stream 2: The actual air temperature and the abundance of the respective group in the preceding month were shown to be significant explanatory variables

	Stream 1						Stream 2					
	Response variable											
Predictor variable	PLANT	HYDR	AMPHI	HELO	NOSP	POTNOD	PLANT	HYDR	AMPHI	HELO	NOSP	POTNOD
AT	.	.	.	.	.	.	***	***	**	*	***	***
AT_{-1}	.	.	.	.	.	***	*	**	.	.	.	***
WT	.	.	.	.	.	.	.	.	.	.	.	.
WT_{-1}	.	.	.	***	***	.	.	.	.	.	***	.
FW	.	.	.	.	.	.	.	*	.	.	.	.
FW_{-1}	.	.	***	.	.	.	.	.	.	.	.	.
WD	***	***	.	.	.	.	.	.	.	.	.	**
WD_{-1}	.	*	.	.	.	.	.	.	.	.	.	.
PLANT	.	.	.	.	.	.	.	.	.	.	.	.
$PLANT_{-1}$	**	.	.	.	.	.	***	.	.	.	.	.
HYDR	.	.	.	.	.	.	.	.	.	.	.	.
$HYDR_{-1}$	.	***	.	.	.	.	.	***	.	.	.	.
AMPH	.	.	.	.	.	.	.	.	.	.	.	.
$AMPH_{-1}$	.	.	.	.	.	.	.	.	***	.	.	.
HELO	.	.	.	.	.	.	.	.	.	.	.	.
$HELO_{-1}$	.	.	.	*	.	.	.	.	.	***	.	.
NOSP	**	*	.	.	.	.	.	.	.	.	.	.
$NOSP_{-1}$	.	.	.	.	***	.	.	.	.	.	***	.
POTNOD	.	.	.	.	.	.	.	.	.	.	.	.
$POTNOD_{-1}$	.	.	.	.	.	.	.	.	.	.	.	***
R^2	0.79	0.76	0.19	0.51	0.64	0.20	0.66	0.63	0.67	0.57	0.73	0.61

Table 1. Significances of the effects of environmental variables and past abundances on the present abundances of individual plant groups based on multiple linear regressions with stepwise selection of predictors

*AT – air temperature, WT – water temperature, FW – flow velocity, WD – water depth, PLANT – total macrophyte abundance, HYDR – abundance of hydrophytes, AMPH – abundance of amphiphytes, HELO – abundance of helophytes, NOSP – number of species, POTNOD – abundance of Potamogeton nodosus, the subscript –1 at the end of abbreviation of environmental variables indicates the value of the respective variable of the preceding month; Significance: * P<0.05, ** P<0.01, *** P<0.001*

for the seasonal dynamics of all studied groups. Three additional explanatory variables proved to be significant: flow velocity for hydrophytes, water temperature in the preceding month for the number of species and water depth for *Potamogeton nodosus* (Table 1). R^2 values are quite similar for all groups, ranging from 0.57 to 0.73 (Table 1).

3.3 Comparison of streams

Culmination of plant abundance: The estimation procedure of the parameters for the nonlinear regression model for amphiphytes in Stream 1 did not converge because of generally very low and randomly varying abundances within sections. Therefore, no comparison for this plant group is possible. Peak of abundance is temporally shifted between streams for all plant groups except helophytes (Table 2). The culmination of plant abundance in Stream 1 occurs approximately one month later than in Stream 2 (Figure 3). However, the shift is not equal for all groups and species. The estimated difference between peak abundances was 0.57 month for the total plant abundance, but 1.43 months for *Potamogeton nodosus*. Species richness also culminated 0.90 month later in Stream 1 compared to Stream 2, although a slight temporal bimodality was observed in Stream 2 (Table 2).

Effects of environmental variables: In both streams, delayed dependence was observed for all groups, but other explanatory variables are different. In the case of total plant mass and the abundance of the dominating group (hydrophytes for Stream 1 and amphiphytes for Stream 2), water depth, and air temperature affected seasonal dynamics, respectively (Table 1).

Macrophyte group	Stream1 Mean ± Standard Error	Stream2 Mean ± Standard Error	t-test
Total abundance (A)	3.56 ± 0.075	2.99 ± 0.201	2.657**
A of hydrophytes	3.60 ± 0.085	2.77 ± 0.142	5.015***
A of amphiphytes	nc	2.86 ± 0.314	.
A of helophytes	3.61 ± 0.111	3.38 ± 0.402	0.551ns
A of *Potamogeton nodosus*	4.10 ± 0.190	2.67 ± 0.133	6.166***
Number of species	3.88 ± 0.172	2.98 ± 0.193	3.481***

Table 2. Time (month) of the peak abundance of macrophyte groups (0 – beginning of May to 6 beginning of November)

*nc – no convergence of the procedure of estimation of nonlinear regression parameters, significance: * P<0.05, ** P<0.01, *** P<0.001, ns – non-significant*

4. Discussion

4.1 Macrophyte species and functional groups and their role on seasonal dynamics of macrophyte abundance

The abundance of macrophytes changed during the vegetation season. In Stream 1, the seasonal fluctuations were moderate for all plant groups as well as for *Potamogeton nodosus*, in contrast to Stream 2 where the abundances were very variable (see the Results section). The abundance fluctuations that we observed within Stream 1 are quite high but comparable to the observation of other authors [12,14,15]. The streams that they studied had, however, quite stable flows, in contrast to those included in this study. In the case of Stream 2, considerable fluctuations can be explained primarily by hydrological changes and the morphology of the bottom: during the vegetation season, a part of flowbed was exposed to air and so the conditions for different groups or species of macrophytes varied along the flow. Anyway, the data found in the present study need to be verified in future studies as only one vegetation season of sampling was carried out.

Abundance of macrophytes in both streams is clearly determined by the dominating group and/or several dominant species and their past abundance (Table 1). For Stream 1, it is the group of hydrophytes and mainly *Sparganium emersum*. For Stream 2, the total plant mass is composed mainly of amphiphytes and the helophyte *Sparganium erectum*, but the proportions of individual aquatic plant groups is much more balanced compared to Stream 1 (see Figure 2). The presence and abundance of individual groups of macrophytes is affected mainly by the river channel morphology, bank inclination, water depth as well as dispersal strategies of plants. Helophytes and amphiphytes dominated in shallow waters near the banks, but decline rapidly with increasing depth and distance to the bank, reflecting the importance of dispersal by ingrowth from populations on the banks into water [21,22]. On the other hand, hydrophytes dominated on intermediate and great depth independently of the distance from the banks, reflecting the lengthwise dispersal in the downstream direction [22]. We made similar observations. Steep banks and deep water did not allow expansion of amphiphytes and helophytes in Stream 1, whereas hydrophytes had optimum conditions for development. In Stream 2, conditions for amphiphytes and helophytes were favourable. *Sparganium emersum* behaved as hydrophyte in Stream 1, although it is frequently classified as an amphiphyte [e.g. 22,23]. Generally, it is a plant of still to fast-flowing watercourses with a moderate to high nutrient status growing in fine (silt-clay) sediment [e.g. 7,24-27]. In the case of Stream 1, it grows both in moderately flowing and eutrophic waters with sand as subtrate. *Sparganium emersum* belongs to species with very good colonisation abilities [28]. *Sparganium erectum* is a typical helophyte species growing in finer (silt, clay or sand) or organic substrates, in still to slow-flowing, shallow to deep, eutrophic waters; it tolerates water level fluctuation [e.g. 24,29,30]. All these conditions were fulfilled in Stream 2, where this species was among the strongly dominant ones.

When comparing the behaviour of individual macrophyte groups between streams, there is a clearly delayed culmination of all groups except helophytes (Figure 3, Table 2). The difference is most pronounced for *Potamogeton nodosus*, reaching maximum abundance in Stream 1 1.5 month later than in Stream 2. *Potamogeton nodosus* belongs to the species preferring deeper waters [24], so that its expansion in Stream 2 was hampered by a rapid water-level decline in the spring below the level necessary for this species. A part of the flowbed was even exposed to air and spots were formed where this species could not survive.

4.2 Effect of environmental characteristics to seasonal dynamics of macrophyte abundance

In addition to plant abundance in the preceding month, water depth and air temperature were found to affect most frequently the seasonal dynamics of total plant mass as well as abundance of individual macrophyte groups or species. In the case of Stream 1, it was mainly water depth which determined total plant abundance as well as abundance of hydrophytes as the dominant macrophyte group. In general, flow regime is one of the crucial factors affecting distribution and abundance of macrophytes in running waters [1,31,32]. The flow regime of Stream 1 exhibited an unusual temporal course. Water depth increased slowly at the beginning of the vegetation season, after that it increased rapidly and culminated in summer months, and subsequently declined abruptly reaching the minimum at the end of the observation period (Figure 1C).

Actual air temperature was the most important explanatory factor in the case of Stream 2. It is closely correlated with water temperature, which has, however, a smoother course. Ambient temperature influences the distribution of aquatic plants by affecting their physiology, including germination of seeds, initiation and rate of seasonal growth, and onset of dormancy [2]. In our case, air temperature maximum clearly overlaps with the culmination of total plant mass as well as the peak abundance of most macrophyte groups and species (Figure 1A, Figure 3). It was air rather than water temperature that was the more dominant factor when explaining abundance of aquatic plants, which may be related to two aspects. First, air temperature may better correlate with other environmental factors affecting plant growth but not directly assessed in this study, e.g., photosynthetic active radiation. Second, helophytes and amphiphytes dominated over hydrophytes in Stream 2. A substantial part of the biomass is exposed to the air in these two macrophyte groups.

The course of flow velocity related to macrophyte abundance and water depth (Figures 1 and 3) differs between streams. In the case of Stream 1, flow velocity decreased with an increase of macrophyte abundance, whereby the culmination of water depth and macrophyte abundance temporally overlapped with the minimum flow velocity. This fully corroborates the observations of other authors, suggesting that growth and die-back of aquatic macrophytes have an effect on the dynamics of flow, demonstrated primarily in decreasing flow velocity caused by the expansion of macrophytes [13,33,34]. There might thus be a positive feedback between aquatic plants and their environment: high density of hydrophytes hampers the flow and causes increasing water level, which in turn provides optimum conditions for the growth and survival of this macrophyte group. However, the increase of water level was mainly due to an increase of the Morava river discharge during the summer 2005, as Stream 1 is connected with the Morava river during higher discharge. In the case of Stream 2, the temporal course was different. Flow velocity decreased along with macrophyte development at the beginning, but later on it increased in spite of their maximum expansion. This can be explained by the narrowing riverbed because of a decreasing water level and exposing part of the bed, whereby a substantial part of macrophytes (helophytes, amphiphytes, and partly even hydrophytes) grew in the dry part of the riverbed and did not hamper water course.

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