

Architectural adaptation in *Myriophyllum spicatum* L. in a lotic environment: is it caused by current velocity?

Ali so spremembe rastne oblike pri vrsti *Myriophyllum spicatum* L. v tekoči vodi posledica hitrosti vodnega toka?

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Abstract: Little information is available for aquatic plants regarding their architectural response to strong environmental drivers like water flow. We examined architectural variability in *Myriophyllum spicatum* L. in the short terminal section of a small canal earlier used for inland navigation. This stretch is characterised by decreasing water depth towards a final spill-over construction, which causes increasing current velocity. Visibly different plant beds had developed at three sampling sites, located between the upstream end of the study reach and the end at the spill-over. This situation bears some resemblance to an experimental flume due to regulated water flow and constant discharge, yet with aquatic plant beds still located in their permanent environment during the whole year. Following this precondition our hypothesis envisaged a close relationship between current velocity and realised plant architecture. Current velocity was measured with an electronic vane device, and representative architectural features of plants were recorded from plant samples at the sites of different flow. Characteristic and significant variation in the architecture of *M. spicatum* was demonstrated at the sites of different current impact. Regarding other environmental parameters like sediment composition, water chemistry or the effect of shading no influence seems likely expected, as samples were collected across the canal width at each site. The mean values of all architectural parameters of *M. spicatum* follow the same trend with high significance, regarding the increase in plant length, branching, and the overall dimension of the plant beds, which is in close relationship to the current velocity at the sampling sites. The few other records available in literature cited in this paper point into the same direction, but these studies were also carried out in the field. In our opinion the clear results may not comply with a final and experimentally generalised relationship between aquatic plant architecture and water flow. But our contribution offers some statistical proof that our hypothesis is not too far from explaining the effects of current velocity, which is one of the main environmental parameters defining aquatic plant growth.

Keywords: aquatic macrophytes, water flow velocity, architectural adaptation, *Myriophyllum spicatum*

Izvleček: O spremembah rastne oblike vodnih rastlin zaradi vodnega toka je malo znanega. Proučili smo variabilnost rastne oblike klasastega rmanca (*Myriophyllum spicatum* L.) v končnem delu kanala, ki se je včasih uporabljal za plovbo. Na 70 m dolgem odseku se globina vode nižja, kar vpliva na povečanje hitrosti vodnega toka. Na treh izbranih vzorčnih mestih vzdolž raziskovanega odseka se sestoji klasastega rmanca razlikujejo že po izgledu. Zato smo predvidevali, da so spremembe v rastni obliki posledica sprememb v hitrosti vodnega toka. Na različnih vzorčnih mestih smo z elektronskim merilcem izmerili hitrost vodnega toka ter analizirali značilnosti rastne oblike vzorcev rastlin. Dokazali smo pomembne razlike v razrasti in velikosti vrste *M. spicatum* na različnih lokacijah. Drugi okoljski dejavniki, kot so sestava sedimenta, kemizem vode in učinek senčenja, niso imeli vpliva na rast rastlin, saj so bili vzorci na vseh lokacijah odvzeti po vsej širini kanala. Povprečne vrednosti vseh merjenih parametrov kot so povečanje dolžine rastlin, stopnja razvejanosti in skupna velikost sestoja, sledijo istemu vzorcu, ki je v tesni povezavi s hitrostjo vodnega toka na območjih vzorčenja. Menimo, da kljub jasnim razlikam v razrasti rastlin ne moremo v celoti potrditi povezave med rastno obliko in hitrostjo vodnega toka.

Ključne besede: vodni makrofiti, hitrost vodnega toka, spremembe rastne oblike, *Myriophyllum spicatum*

Introduction

The architecture of a plant describes the spatial organisation of its structures in three dimensions, which is under genetic control (Reinhardt and Kuhlemeier 2002), often producing a characteristic branching pattern most easily observed even by non-experts. But exogenous constraints (Barthélémy and Caraglio 2007) determine the ontogenetic result of plant development leading to architectural variation (temperature stress: Bridge et al. 2013, planting density: Costes et al. 2012, shading: Winona 2015, Ford 2014, McKenzie-Gopsill et al. 2016)

All the examples cited above deal with terrestrial plants. Much less information is available for aquatic plant species. This is especially true when looking at the effects of water flow on aquatic plant architecture.

One of the earliest sources is information provided in Arber's (1920) study on aquatic plants. The central focus is given to leaf types regarding heterophylly, land and water forms, entire, dissected, fenestrated, cylindrical or ribbon-shaped leaves, as well as several other aspects of leaf composition. Some relation to architectural aspects is found in a comment on submerged leaves and side branches, where the

development of 'juvenile-like' leaves was detected. Butcher (1933) covered the influence of water flow regarding some aspects of water chemistry and substrate (ibid. p.63), and described seasonal and inter-annual changes in species composition and cover (ibid. p.80, R. Itchen, and p.81, R. Lark), but no mention is made of phenotypic plasticity related to the water current.

In Sculthorpe's (1967) book on the biology of vascular aquatic plants the influence of water current is mentioned, with a focus on anatomical features of macrophyte leaves. But a short note refers to leaf segments of *Myriophyllum* (no species cited) being 'shorter and firmer in flowing water' (ibid., p.109). Phenotypic variation was detected in aquatic *Ranunculus* species and in the genus *Potamogeton*, where current speed was related to variable leaf form and anatomy (ibid., p. 221/222). A perpetuated juvenile status of leaves was observed in some species of *Alisma*, *Potamogeton*, *Sagittaria* and *Sparganium* (ibid., p.232) under the impact of swift current.

Abundant information on aquatic plants and their response to a range of environmental conditions is provided in the books of Haslam (1987, 2006, 2013). The relation of aquatic macrophytes and flow conditions is covered in many diagrams, tables and drawings showing typical groups and

situations, especially those of weed beds in rivers of different character (e.g. geological background, slope, discharge, etc.). Specifically regarding *Myriophyllum spicatum* L., this species was found to be most abundant in moderate flow, but showed a marked ability to withstand fast flow as well. Among several species recorded to tolerate spates *M. spicatum* was cited as not being uprooted as easily as others. Unfortunately no numerical information on current speed is provided, and no reference to details of plant architecture is made. However, in her recent book on river plants Haslam (2013, p.71 f.) adds some architectural information regarding greater length of internodes and more elongated plants in older parts of rheophilic (i.e. current-affine) *Ranunculus* beds, and growing in greater water depth.

Gessner (1955) remains a useful source of information on the relationship between current velocity and architectural parameters for *Nuphar lutea* (L.) Sm. and *Berula erecta* (Huds.) Cov. (name used by Gessner, *ibid.* p.303: *B. angustifolia*).

Regarding specific information on *M. spicatum*, Whitton (1975, p.111) mentions that this species may produce smaller plants in faster flow. Miler et al. (2014) compared the biomechanical properties and morphological characteristics of lake and river plants, but *M. spicatum* samples were taken from still waters (lakes, ponds) as opposed to *M. alterniflorum* DC., which was sampled from rivers. These results relate to the architectural data reported by Wegleiter (1990), who studied *M. spicatum* in lakes of South-Tyrol (Italy), and do not correspond to our samples collected from sites in running water.

The information cited above shows that there is little quantitative data on the architecture of aquatic plants in relation to water flow in the literature. Our study aims at testing the hypothesis that variation in architectural features of *Myriophyllum spicatum* L., may be influenced by current velocity.

Sampling Site

The ‘Wiener Neustädter Kanal’ (Wiener Neustädter Canal, WNC), was selected as the study location, where easily visible differences in form and size of *Myriophyllum spicatum* L. beds attracted our interest.

Opened in 1803, this canal, originally 61 km long, connected Wiener Neustadt (Federal Province of Lower Austria) and the Centre of Vienna as the only part of a commercial transport canal system that was originally planned to reach Trieste/Italy (Lange 2003).

The canal receives its water from a stream that originates in alpine catchments, and the discharge is controlled by a main weir at Wiener Neustadt, where the canal is diverted from the source stream. The regulated flow and minor changes in discharge bear resemblance to an experimental flume, regarding other environmental features (nutrients, sediment type etc.), too.

Due to its rather constant flow the WNC provides favourable conditions for macrophyte development, which causes maintenance activities including some mechanical management of submersed aquatic species, usually located in the upper and middle reaches.

By 1878 the navigation was shut down due to competition from railway freight transport (Bruckmüller et al. 2004). In the early 1970s the canal was terminated at the town of Biedermansdorf, truncating the water course to a length of 36km. Environmental purposes and leisure dominate the present use, but eight small hydropower plants replace former lock sites. The water of the canal spills into a small regulated river, the Mödlingbach (Fig. 1).

The study site was situated in the terminal reach of the WNC (Fig. 1). Three sampling sites showing easily visible differences in plant bed structure, and characterised by different current velocities, were selected in a stretch of less than 70 m.

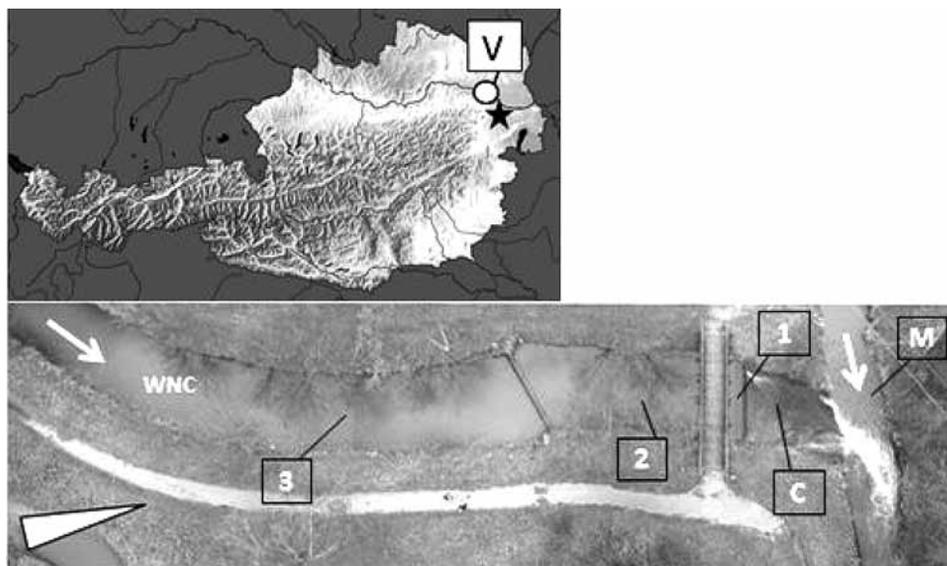


Figure 1: Sampling site.

Upper Panel: V – Location of Vienna; Five-pointed star: location of the study site. Map source: Creative Commons Attribution 3.0 Licence; <http://www.ginkgomaps.com>.

Lower panel: Sampling Sites 1, 2, 3. M: Mödlingbach, receiving the WNC. C: steep chute connecting the WRC with Mödlingbach. Prior to the termination at Biedermannsdorf an aqueduct had led the canal across this stream bed. The upper rim of the chute is a level concrete beam of c. 0.4 m width, crossing the whole course of the WNC, which protects the upper end of the chute against erosion. Arrows indicate flow direction. Triangle: north arrow. All sites are open to the South, ensuring little effect of shading. Image: FDG Austria, DI Norbert Exler, PhD © 2016. All plant samples were collected from the upstream end of the plant beds, where water flow exerts its full force.

Slika 1: Mesto raziskav.

Zgornja slika: V - Mesto Dunaj; zvezica: mesto vzorčenja. Vir Map: Creative Commons 3.0 Dovoljenje; <http://www.ginkgomaps.com>.

Spodnja slika: Mesta vzorčenja 1, 2, 3 M: Mödlingbach, ki prejema WNC. C: strm žleb, ki povezuje WRC s vodotokom Mödlingbach. V kraju Biedermannsdorf je v preteklosti akvadukt vodil kanal preko struge. Zgornji rob žleba je 0,4 m širok. Puščice kažejo smer toka. Trikotnik: Severna usmerjenost. Vsa mesta vzorčenja so orientirana južno, kar zagotavlja odsotnost senčenja. Vir: FDG Avstrija, DI Norbert Exler, PhD © 2016. Vsi vzorci rastlin so bili nabrani gorvodno, kjer vodni tok doseže svojo polno hitrost.

Site 1 is situated at the pedestrian bridge at the upper end of the chute. The concrete beam across the whole canal width provides a level base for current measurement (Fig. 1). At the vertical upstream face of the beam the bottom of the canal rises to a depth of just 0.11 m, due to sediment accumulation at this barrier, forcing the water across its top. This results in an increase in current velocity over the top of the beam (mean current velocity: 1.44 m s^{-1} , S.D. 0.20; $n = 15$ across the canal; specification of the measuring device: see below) before the water starts rushing down the

chute. At this site 6 complete plants of *M. spicatum* were sampled for architectural measurement.

Site 2 is located in a short reach of quite abundant plant growth in a section between 8 to 15 m upstream of Site 1. This part of the canal is characterised by 0.30 m mean water depth (S.D. 0.08) and a mean current velocity of 0.92 m s^{-1} (S.D. 0.26). At this site 4 samples were collected.

Site 3 is located in a reach 45 to 65 m upstream of Site 1 where very large plant stands had developed. The characteristic features of this site are 0.32 m mean water depth (S.D. 0.14) and a

mean current velocity of 0.39 ms^{-1} (S.D. 0.05) in the peripherals of the plant stands. At this site 5 samples of *M. spicatum* were collected, growing closer to the right bank.

Methods

Measurement of current velocity

Current velocities were measured at the sampling sites with an electronic flow meter (Type μP – ASDI; vane diameter: 16 mm; Höntzsch GmbH, Waiblingen, Germany). The small diameter of the vane allowed for setting the probe close to either the canal surface or bottom or very close to the plant stands, respectively.

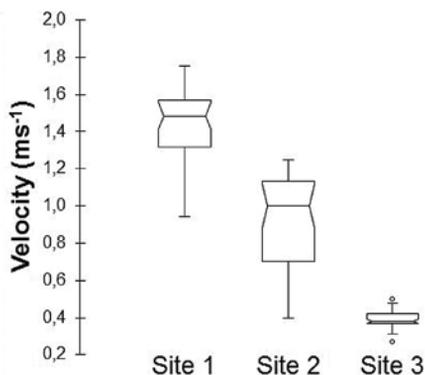


Figure 2: Current velocities across the canal at the three sampling sites.

Box: Median; 25 and 75% Quartile; Whiskers: Min/Max (Significance: Kruskal-Wallis-Test: $p < 0.0001$ for all combinations of the three Sites); Circles: outliers.

Slika 2: Hitrosti vodnega toka na treh mestih vzorčenja.

Okvir: Mediana; 25 in 75 % četrtine; Brki: Min / Max (Značilnost razlik: Kruskal-Wallis-test: $p < 0,0001$ za vse kombinacije); krožci: izstopajoči podatki.

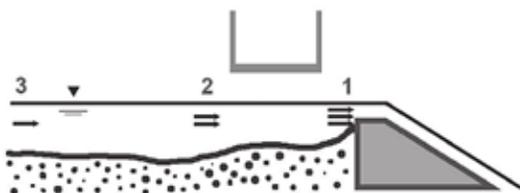


Figure 3: Location of sampling sites, concrete bar and chute (schematic).

The water level is indicated by the triangle. Arrows indicate increasing current velocity. The concrete bar and the chute are located to the right. Actual water depth on top of the bar: 0.17 m. Position of water level, width of the concrete bar top and canal bottom (depth related to the middle of the water body) are approximated to the real situation, including the pedestrian bridge. The average gradient of the chute is 18.1%.

Slika 3: Lokacija mest vzorčevanja (shema).

Vodostaj je označen s trikotnikom. Puščice kažejo povečanje hitrosti toka. Betonski preliv in žleb se nahajata na desni. Globina vode na vrh: 0,17 m. Položaj vodostaja, širina betonskega preliva ter zgornji in spodnji del kanala (globina je sorazmerna s sredino vodnega telesa) je prikaz dejanskega stanja, vključno z mostom za pešce. Povprečni naklon žleba je 18,1 %.

Selection of the tested species

Due to the regulated conditions in the WNC neither water chemistry nor discharge show high variability, except for periods of closure of canal parts for repair and maintenance, or during aquatic plant removal, which is not conducted very frequently and never over the complete canal length at a time. Such conditions favour macrophyte growth, but only a few species have established in this artificial water body on a rather permanent basis.

The first macrophyte surveys covering the full length of the WNC were carried out in 1992 and 1994 (Janauer, unpublished). In 1992 the occurrence of *Elodea canadensis* Michx., *M. spicatum*, *Potamogeton crispus* L., *P. pectinatus* L. [syn. *Stuckenia pectinata* (L.) Börner], *P. perfoliatus* L., and *Ranunculus trichophyllus* Chaix was recorded. In 1994 *E. canadensis*, *M. spicatum*, *P. pectinatus*, *P. perfoliatus*, *R. trichophyllus*, and *Zannichellia palustris* L. were detected. In Gasteiner's survey of 1999 (Diploma Thesis, 2001), *M. spicatum* was the macrophyte species with highest frequency regarding the number of survey units over many years (Frequency: 1992 – 35.1; 1994 – 39.2; 1999 – 48.9).

The samples taken at the three sites were the complete plants at Site 1, but since Site 2 and 3 were subject to slower water flow, larger beds of plants were present. From these beds, individual fully grown plants were collected, which consisted of a central axis, rooted at some length, and the respective branches of different order.

The samples were transported in pails of water to a nearby location, where the material was spread out on a large table covered with plastic film. Location and hierarchy of branching (Bornkamm et al. 1991) was recorded with a metal tape measure, to assess the architectural structure of each plant sampled. The axes and branches of terrestrial plants display a stable structure which can be described mathematically (Godin et al. 1999). Submersed aquatic plant stands – the 'waving plants of the river' (Haslam 2013) – move constantly following the flow and turbulence of the water, and a fixed three dimensional geometry cannot be defined *in situ*. We focused on several parameters of the branching pattern as an indicator of variation in plant architecture related to water flow velocity.

Statistics

Based on measuring and categorising individual features of the plant architecture the data were analysed with SPSS 15.0 for WINDOWS. Normal distribution was tested by applying Kolmogorov-Smirnov, or Shapiro-Wilks tests, respectively. ANOVA was applied to normally-distributed data together with Duncan Post-Hoc mean separation test, testing for significance between means. For testing the significance of non-normal data Kruskal-Wallis test was used, followed by the Mann-Whitney-U-Test to discriminate between significantly different categories. Methods followed Untersteiner (2007, pp. 133-182). We used the following references as a nomenclature sources: Casper and Krausch (1980), Casper and Krausch (1981) and The Plant List, 2010. Version 1. <http://www.theplantlist.org/>.

Results

Typical examples of *Myriophyllum spicatum* architecture are shown below, which are characteristic for the three sampling sites and the effect of current velocity (Fig. 4).

Characteristic examples of growth form at Sites 1-3

The following passage shows the relationship between different architectural characteristics assessed for *Myriophyllum spicatum* at the three sampling sites. Significance of differences is shown in Table 2.

Length of the main stem and Total length of all axes

Length of the main stem regards BO 1 axes (BO = branching order), which covers all sampled individuals at a Sampling Site. Total length of all axes combines main stem length plus all branches (BO 1-5)

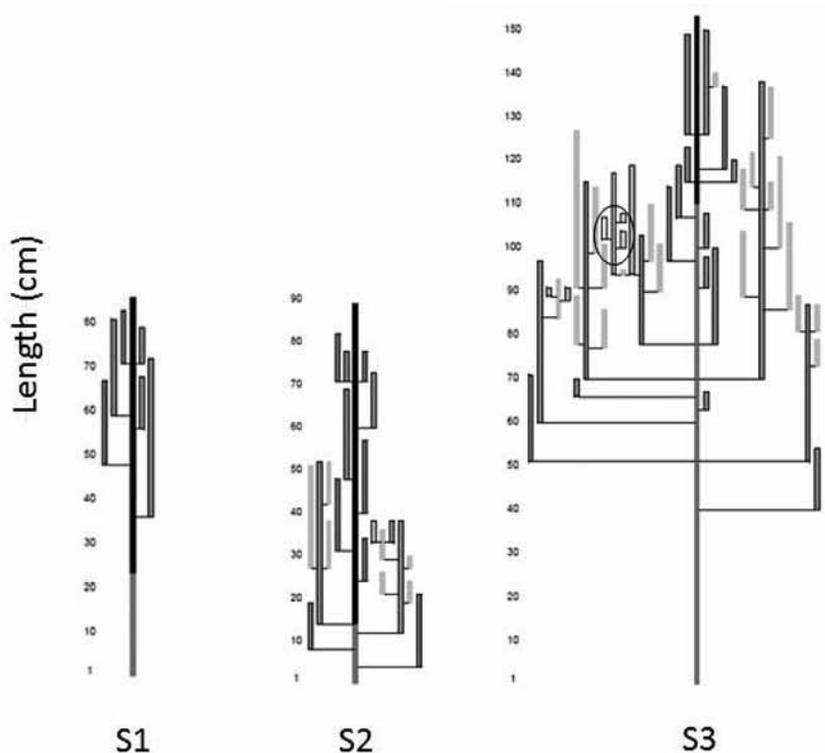


Figure 4: *Myriophyllum spicatum* - Examples of branching at Sites 1 – 3

BO = branching order. Grey: BO 1 – main stem, rooted; Black: BO 1 – main stem, floating; Dark Grey, black outline: BO 2; Light Grey, no outline: BO 3; White, black outline: BO 4; Additional branches on BO 4 axis: BO 5 (marked by oval shape).

S1: High current velocity impact. Few branches developed. S2: Intermediate current velocity impact. The central bulk of the bed is composed of BO 2 and BO 3. S3: Lower current velocity impact. Note the extremely short BO 3 axis between the two BO 4 axes. The left one developed three short BO 5 branches.

Slika 4: *Myriophyllum spicatum* - Primeri razvejanosti na lokacijah 1 - 3

BO = stopnja razvejanosti, temno sivo: BO 1 - glavno steblo - ukoreninjeno; črno: BO 1 - glavno steblo, plavajoče; temno sivo, črno obrobljeno: BO 2; svetlo sivo, neobkroženo: BO 3; belo, črno obrobljeno: BO 4; dodatne veje na BO 4. osi: BO 5 (obkroženo). S1: velik vpliv hitrosti toka. Razvejanost majhna. S2: srednji vpliv hitrosti toka. Osrednji del sestoji je sestavljen iz BO 2 in BO 3. S3: majhen vpliv hitrosti toka. Izjemno kratka BO 3 os med dvema BO 4 osema. Na levi so razvite tri kratke BO 5 veje.

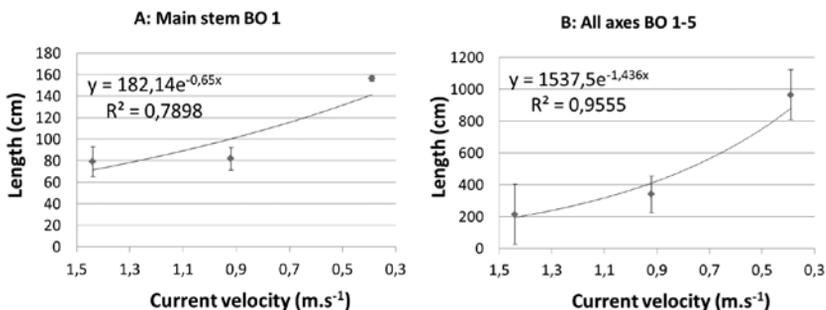


Figure 5: (A): Main stem (BO 1) – Length (B): All axes (BO 1 – 5) - Length
Regarding all Figures: $n_{\text{Site 1}} = 6$, $n_{\text{Site 2}} = 4$, $n_{\text{Site 3}} = 3$. Whiskers: S.D., $p = 0,05$; Significance: see Table 1. Regression line: exponential.

Slika 5: (A): Glavno steblo (BO 1) – dolžina (B): vse osi (BO 1 – 5) - dolžina
($n_{\text{Site 1}} = 6$, $n_{\text{Site 2}} = 4$, $n_{\text{Site 3}} = 3$). Brki: S.D., $p = 0,05$; Značilne razlike: glej Tabelo 1. Regresijska premica: eksponentna.

Figure 5A shows that the main stem (BO 1) of sampled individuals increases in length with increasing distance from the downstream end of the canal, which is equivalent to decreasing current velocity. The main stems of Site 1 and 2 are very similar regarding the mean, but S.D. is smaller at Site 2. The length of main stems (BO 1) at Site 3 is significantly longer than that of Site 2, which is not significantly different from Site 1.

In Figure 5B the means of Site 1 and Site 2 are still closely related, but Site 3 is clearly different from the other sites.

Total number of branches (BO 2 – 5)

The development of branches is a conspicuously different feature of the plants sampled at the

three sampling sites, related to the change from fast to slower water flow.

The distances between the means of Sites 1 and 2 are larger for branches than for main stems but the S.D. values are overlapping. The number of branches at Site 3 is significantly higher than that of Site 1 and 2.

During the examination of the sampled material it became obvious that some of the branches (BO 2 – 5) showed no furcation, i.e. no further branching, representing terminal axes, often of considerable length. In contrast other branches of lower, as well as higher BO level had developed additional branches. These two types of branches were analysed separately.

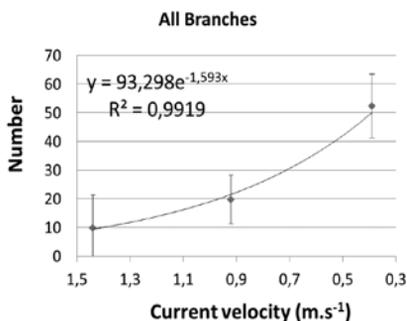


Figure 6: Total number of branches (BO 2-5).

Slika 6: Skupno število stranskih poganjkov (BO 5/2).

Branches without furcation – terminal axes

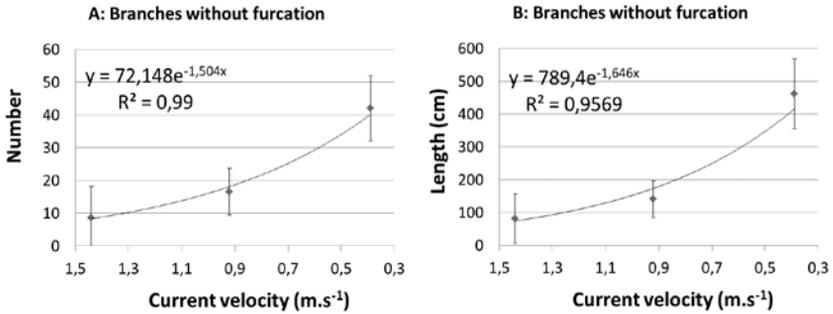


Figure 7: Branches (BO 2 – 5) without furcation – (A) number, (B) length.
 Slika 7: Stranski poganjki (BO 2 – 5) brez razvejanja – (A) število, (B) dolžina.

The number of BO 2 – 5 terminal axes (Fig. 7A and B) increased from the location with fastest flow towards the one with the slowest. Sites 1 and 2 did not show significant difference, but the samples at Site 3 were significantly separated regarding both the number and the length of these branches (Table 2).

Branches (BO 2 – 4 -type) with furcation

When viewing individual beds of *M. spicatum* in the WNC from the bank the intensive development of bed size was instantly recognised for locations with decreasing flow velocity. This feature is caused by additional branching of BO

2 – 4 -type branches. The examples of characteristic individual plants given in Figure 8 clearly show that effect.

Branches of BO 2 – 4 -type producing branches of higher order (BO 3 – 5) define, in part, the overall size of the beds of *M. spicatum*. The means in Figure 8 are clearly separated and indicate the intensive development of additional axes, which increase the visual bulk of beds in locations with lower impact of current velocity. Despite the relatively high variation in branching of individual plants sampled from the sites statistical analysis (Table 2) reveals some significant differences.

Significance of the results shown in Figures 5 – 8 is presented in Table 2.

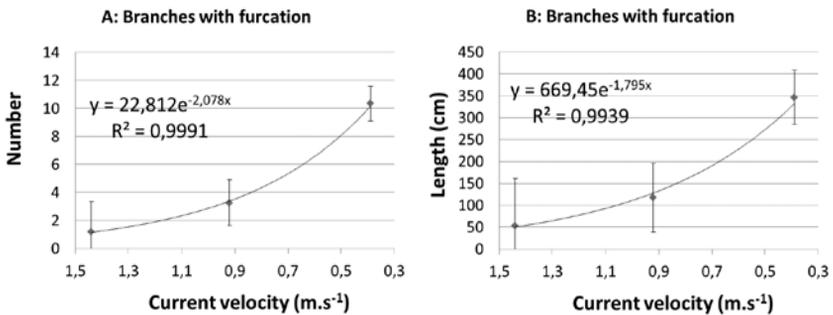


Figure 8: Branches (BO 2 – 4) with furcation – (A) number, (B) length. Consider the different scale of the ordinate, as compared to Fig. 7.
 Slika 8: Stranski poganjki (BO 2-5) z razvejanjem – (A) število, (B) dolžina. Ordinate se razlikujejo v primerjavi s sliko 7.

Table 2: Relationship of architectural parameters of *Myriophyllum spicatum* Sampling Sites 1, 2, 3 (means); Square brackets: Figure number. t. a.*: terminal axes without furcation. Different letters indicate significant difference ($p = 0.05$).

Tabela 2: Razlike v razraslosti rastlin vrste *Myriophyllum spicatum* na različnih mestih vzorčenja. Mesta vzorčenja: 1, 2, 3 (srednje vrednosti); Oglati oklepaji: Številka slike. t. a. *. os brez razvejanja. Različne črke kažejo pomembne razlike ($p = 0,05$).

Architectural parameters	Differences among sampling sites		
Main stem (BO 1) – length [5A]	1 ^a	2 ^a	3 ^b
All axes (BO 1 – 5) – cumulated length [5B]	1 ^a	2 ^a	3 ^b
Branches (BO 2 – 5) – total number [6]	1 ^a	2 ^a	3 ^b
Branches (BO 2 – 5) / t. a.* – number [7A]	1 ^a	2 ^a	3 ^b
Branches (BO 2 – 5) / t. a.* – length [7B]	1 ^a	2 ^a	3 ^b
Branches (BO 2 – 4) / furcate – number [8A]	1 ^a	2 ^a	3 ^b
Branches (BO 2 – 4) / furcate – length [8B]	1 ^a	2 ^a	3 ^b

Discussion

Myriophyllum spicatum L. is a widespread aquatic plant, with a potential to inhabit still, as well as running water bodies. When comparing the architectural features of *M. spicatum* in lakes (Wegleiter 1990) and that recorded in our survey of the Wiener Neustädter Canal (WNC), the phenotypic differences in *M. spicatum* had become evident. This triggered our interest in the final reach of the WNC, where flow conditions change markedly over a rather short distance and phenotypic plasticity was apparent in the size of the plant beds, as well as in the architectural variation we had studied then.

In general all the parameters tested in this study reacted quite similar regarding the architectural features, especially when comparing the mean values at each sampling site. This fact is obviously expressed by the regression lines in Figures 5 – 8. But tests revealed that plant features were not

significantly different for Site 1 and Site 2 (Tab. 2). Site 3, in contrast, was clearly different from the other two sampling sites. As the difference is highly significant in current velocity at all three sites one can reflect on the different results recorded for the architectural parameters at Sites 1 and 2. Since different individuals were sampled across the width of the canal this caused a greater standard deviation and no significance ($p = 0.05$) when compared to that of the current velocity. On the other hand this stronger scatter in plant architecture may provide different micro-scale habitats for organisms associated with plant beds.

A comparison of our data with results from a still water can illustrate possible differences in two architectural features of *M. spicatum*: Length of the main stem (BO 1-type) and the Length of Internodes (Table 3; both parameters recommended by Lehmann et al., 1997; results reported below: Wegleiter, 1990, pp. 77-79, Montiggler See, South Tyrol, Italy).

Table 3: *Myriophyllum spicatum* - Comparison of architectural parameters in still (Montiggler Lake) and running water (WNC)

Range of main stem length and mean internode length

Tabela 3: *Myriophyllum spicatum* - primerjava arhitekturnih parametrov med stoječo (Montiggler jezera) in tekočo vodo (WNC)

Obseg dolžine glavnega stebela in povprečna dolžina internodija

Date	Montiggler Lake		Sites	Wiener Neustädter Canal (this study)	
	Main stem ¹ (m)	Internodes ² (cm)		Main stem ² (m)	Internodes ² (cm)
15.7.1986	0.75 - 0.9	2.17	1	0.79	2.36
12.8.1986	1.10 - 1.35	2.24	2	0.81	2.42
12.9.1986	1.75 - 1.90	2.78	3	1.56	6.17
3.10.1986	2.30 - 2.40	3.38			

¹ range, ²mean

The mean length of the main stem of the WNC samples at Site 1 and 2 is about equivalent to that of early summer samples from the lake. Main stems of Site 3, the longest in the WNC, are considerably shorter than those in the lake during the final summer period. On the other hand, under flow stress in the WNC the length of internodes is greater than that in the lake. These examples indicate substantial differences in architectural adaptation to still as opposed to running water conditions, in *M. spicatum*.

One of the most conspicuous features of the reaction of *M. spicatum* beds to decreasing flow velocity in the WNC is the increase in general bulk, which shows the relationship between 'biomass density and plant architecture', according to Duarte and Roff (1991), who also studied *M. spicatum*. When analysing the causes for that phenomenon the types of branches provide answers for the samples collected at the WNC. Figure 4 provides graphic examples of this phenomenon and Figure 6 shows the total number of branches recorded (Branching Order, BO 2 – 5). Two groups showing 'bulk production' were easily differentiated as part of the BO 2 – 5 sample. The first group is characterised by branches directly emerging from the main axis (BO 2), as well as from branches of higher order (BO 3 – 5), which failed in producing additional

axes and ended up as axes without furcation or 'terminal axes' (Fig. 7A, 7B). The second group comprises axes of BO 2 to BO 4-type, which produced additional branches (Fig. 8A, 8B). The effect of slower water flow effectively results in additional bulk production. This is in full accord with the findings of Chambers et al. (1991), who showed that even a modest increase in water flow decreased the biomass and abundance of aquatic weed beds, providing proof with experimental transplants. Hrivnák et al. (2013) also listed flow regime prior to fine substrate as the most important driver for species and environmental conditions relationship.

Searching for much earlier information on flow impact affecting aquatic plants Gessner's (1955) examples are in full support with our results, as shown in the following citation on two macrophytes of different growth form. Though not listing *M. spicatum* among rheophobiont [associated with faster flow] aquatic species (70 – 120 cm.sec⁻¹), nor those occurring in more moderate flow (13 – 70 cm.sec⁻¹) either, this author reports a general restraint on stem, internode and leaf length by faster flow (ibid. p.302), indicating '*Myriophyllum*' without defining the species (Tab. 4, after Ruess, probably by personal communication to Gessner, as Ruess is not listed in Gessner's references).

Table 4: Attenuation of plant parameters in *Myriophyllum sp.* related to water flow
Categories and numbering format according to the source. * no record.

Tabela 4: Spremembe parametrov rastlin pri vrsti *Myriophyllum sp.* v povezavi s pretokom vode. Kategorije in vrednosti glede na vir. * ni podatka.

Water flow (cm s ⁻¹)	Length of stem (cm)	Internode length (cm)	Leaf length (cm)
0	-*	3 - 6	2.5
20	100	2 - 3	2
70	50	1.5 - 2.0	1.2-1.5

Another example, quite identically referred to in several textbooks, is found in the same source (Gessner 1955, p.305) for petiole length and leave size of *Nuphar lutea* (L.) Sm., regarding the high flow impact at the upstream end of the plant stand (described as 'luv', no numerical values provided), and sites with lower flow within the same plant stand drawn by Gessner (after Ruess, personal communication). Despite missing a differentiation between submersed and floating leaves of this species the essence of the contribution is clear (Tab.5).

In her most recent book Haslam (2013, p.24) referred to the reduction of hydraulic resistance by shorter shoot length and a lack of branching in *Ranunculus peltatus* Schrank. Haslam (2013, p.188) also reports about *R. fluitans* Lam. showing shoots 'barely branched' while being affected by 'torrential' flow, but adapting to a 'well branched' status with 'much longer shoots' after installation of a sluice upstream which reduced flow. This example compares well with our experience in the WNC, where fast flow resulted in barely branched plants at Site 1 and much longer and well-branched plants at Site 3. But, following the same source, when

torrential flow was restored, the beds ('clumps' *sensu* Haslam) returned to their original 'barely branched' form over some time, indicating the phenotypic plasticity of aquatic plants.

Our own data on the impact of different flow velocities, as well as Haslam's example of development, and successive reduction in plant bulk, indicate the importance, and capacity, of aquatic macrophytes to falling back on architectural variation for sustaining survival under variable environmental conditions. According to Grosfeld et al. (1999) such effects may help to distinguish ontogenetic variation from environmental plasticity, as shown by their studies on *Araucaria araucana* (Molina) K.Koch. This aspect was also discussed by Dingkuhn et al. (2005), seeking solutions with simulation models. Stein and Boyer (2006) also proposed ontogenetic drivers like environmental boundary conditions determining the final architecture realised by an individual plant. This should, with respect to the phylogenetic potential in general, enable a plant to adapt to variable conditions of habitat, which are the drivers behind the effects of flow on *M. spicatum* shown in our study.

Table 5: Impact of flow on architectural features of *Nuphar lutea* (L.) Sm.
Numbering format according to the source.

Tabela 5: Vpliv toka na arhitekturne značilnosti vrste *Nuphar lutea* (L.) Sm.
Vrednosti so podane kot v viru.

Flow impact	Petiole length*	Leaf length*	Leaf width*
'luv'= upstream end	5	4.5	5
within stand	25 - 30	9.5	14

* in cm

On the same basis Wolfe and Mazer (2005) argued that the responses to environmental heterogeneity are related to fitness against variable habitat conditions. Following the same line of arguments, but referring to examples of terrestrial plants, Barthelemy and Caraglio (2007) state that genetic determination of architectural features of a species is affected by the environment 'only under extreme ecological conditions' (e.g. determining the crown physiognomy of trees, *ibid.* p.387 and p. 390), and the final expression of structure and architectural position of a particular plant element 'may be modulated by environmental or technical factors' (*ibid.* p. 396). According to this consideration substantial changes in environmental conditions and subsequent architectural adaptation are linked to enable the survival of plant species under pressure of mechanical forces, as described by Puijalon et al. (2011) for wind in terrestrial habitats. Barthelemy and Caraglio (2007) cited 'extreme ecological conditions' as causing variation in plant architecture: when comparing the different density of air and water it does not seem unlikely to expect strong effects of water flow at higher current velocities on aquatic plant architecture. At least currents recorded at the Sites 1 and 2 in this study will exclude the occurrence of many macrophyte species common in the majority of running waters, and phenotypic plasticity (Dingkuhn et al. 2005) may support *M. spicatum* in sustaining current impact in our test sites.

Summary

Information focusing on architectural features of aquatic macrophytes in running water has been rather scarce, which triggered the authors' interest on *Myriophyllum spicatum* L. growing in a part of the Wiener Neustädter Canal (WNC), which provides 'quasi-experimental' conditions due to the almost constant discharge, very uniform other environmental conditions, and significantly different flow conditions caused by technical adaptations in its very final stretch.

Results show that architectural variation of *M. spicatum* is closely related to water flow, yielding

the most reduced growth form at the site with the highest current velocity. Comparison with older and more recent literature points into the same direction in most cases, but the present results comprise the first detailed record on architectural adaptation of *M. spicatum* in running water. In accord with the conception of other authors, this study shows that intensive environmental impact of increasing current velocity at the test sites occurs together with a marked variation in the basic architectural concept in this aquatic plant species. It seems worth trying to confirm this insight with other aquatic macrophytes, too.

Povzetek

Raziskave o arhitekturnih značilnostih vodnih makrofitov v tekočih vodah so redke, zato smo raziskovali zgradbo poganjkov vrste *Myriophyllum spicatum* L., ki raste v delu kanala Wiener Neustädter (WNC). V kanalu so bile prisotne ugodne razmere primerne za izvedbo poskusa, zaradi skoraj konstantnega odtoka, podobnih okoljskih razmer, in zelo različne hitrosti vodnega toka.

Rezultati kažejo, da so spremembe v razrasti klasastega rmanca tesno povezane s hitrostjo vodnega toka. Najmajše in najmanj razrasle rastline so uspevale na mestu z najvišjo hitrostjo vodnega toka. Primerjava rezultatov s starejšimi in novejšimi viri kaže podobne odzive v prilagajanju rastnih oblik, vendar rezultati naše študije podajajo prve natančne podatke o prilagoditvah rastne oblike potopljene rste *M. spicatum* na tekočo vodo. V skladu z drugimi avtorji, je študija pokazala jasen vpliv hitrosti vodnega toka na testnih lokacijah, skupaj s spremembo osnovnega koncepta razrasti vodnih rastlinskih vrst. Te rezultate bi bilo potrebno preveriti tudi na drugih vrstah vodnih makrofitov,

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