



Short communication

Stream flow velocity alters submerged macrophyte morphology and cascading interactions among associated invertebrate and periphyton assemblages



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ABSTRACT

Submerged macrophytes play a key role in the functioning of stream ecosystems since they strongly affect the biological and physical environment of the habitat. On the other hand, flow velocity may affect growth and establishment of submerged macrophytes in streams and rivers. However, little attention has been paid to the morphological responses of submerged macrophytes to different stream flows and in the present study we investigate the intraspecific difference in flow adaptation of a common submerged macrophyte, *Myriophyllum spicatum* L. We found no difference in length of main shoot or total length of lateral shoots of *M. spicatum* plants grown at high and low stream flow. However, shoot and root dry weight biomass, number of lateral shoots, degree of branching and stem diameter of the main shoot increased significantly with increasing water velocity. In contrast, the opposite trend was observed for leaf whorl area and distances between the internodes of the main shoot. The amount of periphytic algae also decreased with increased water velocity, whereas the macroinvertebrate abundances were nine fold higher at high than at low stream flow, suggesting that grazing may, besides higher stream flow, have been a process behind the lower periphyton growth at high flow. Hence, stream flow not only acts as a stress factor leading to morphological changes in submerged macrophytes, but also induces cascading trophic interactions among periphytic algae and invertebrate assemblages, thereby being a major force in shaping the organism communities of streams and rivers.

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1. Introduction

Macrophytes are an important component of aquatic ecosystems by providing habitats and structural diversity for periphyton, invertebrates and feeding areas for predators (Janauer and Dokulil, 2006; Gomes et al., 2012). Hence, macrophytes play a key role in the functioning of stream ecosystems, and may also affect the flow velocity of streams and rivers (Franklin et al., 2008). However, the flow velocity may also affect macrophyte establishment (Riis and Biggs, 2003) and morphology, although this issue is not as well investigated as, for example, the effects of currents and waves in marine ecosystem (Schutten et al., 2005). Macrophytes face significant drag forces imposed by the running water which cause mechanical damage and uprooting (Sand-Jensen, 2003). Puijalon and Bornette (2004) reported that the response of plant traits was

opposite for two macrophyte species with increased flow velocity, illustrating the importance of studying morphological responses of individual species at different flow velocities. The main adaptive morphological response of macrophytes to flow stress would be reducing the risk of uprooting and drag by increasing the root length or root area. Drag can also be reduced by different morphological adaptations, such as changes in plant height, shoot flexibility, leaf area, leaf number, total plant biomass and stem diameter (Sand-Jensen, 2003; Puijalon and Bornette, 2004; Boeger and Poulson, 2003).

Besides stream flow, periphyton communities may affect the growth of submerged macrophytes by reducing the light intensity and uptake of nutrients and dissolved inorganic carbon. Hence, periphyton communities along with stream flow may have a very strong influence on the growth of submerged macrophytes.

Macrophytes and stream flow also play important roles in shaping the assemblage of macroinvertebrates, which has been shown to be highest at flow velocities ranging from 0.3 to 1.2 m s⁻¹ (Beauger et al., 2006). In addition to flow velocity, macrophyte cover has been shown to be positively correlated with

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macroinvertebrate abundances (Verdonschot et al., 2012), and plants with finely dissected leaves and intricate branching often harbor more macroinvertebrates (Walker et al., 2013). Hence, stream flow velocity may indirectly influence the macroinvertebrate community through shaping the morphology of macrophytes.

In order to disentangle the interactions between stream flow, macrophyte morphology and invertebrate abundances in streams, we investigated the intraspecific differences in the adaptation of a common submerged macrophyte, *Myriophyllum spicatum* L., at two different flow velocities. In addition, we assessed the growth of periphyton on the plants and the associated invertebrate assemblage. The initial hypotheses were that (1) the length of plant shoots, plant biomass, leaf area and number of leaf whorls will decrease with increasing flow velocity, (2) there will be less periphytic algae growing on macrophytes at higher flow velocity, (3) there will be higher abundances of macroinvertebrates at low, compared to higher, stream flow.

2. Materials and methods

Our study was conducted in a stream close to Lund, Sweden (55°42'49.49"N, 13°12'28.16"E) between 20th June, 2013 and 6th September, 2013. Two sites having different flow velocities were selected for the experimental growth of macrophytes. The average flow velocity of the selected sites during the experiment was 0.04 (SD, 0.022) m s⁻¹; 0.20 (SD, 0.049) m s⁻¹, which were considered as low and high flow velocity, respectively, (Boeger and Poulson, 2003). The mean water temperature during the experimental period was 18.8 (SD, 1.3) °C. The amount of light received by the *M. spicatum* shoots was measured every second hour between 10:30 and 18:30 a clear, sunny day. The total amount of light received by the plant shoots at high and slow flow was 763 and 457 (μmol m⁻² s⁻¹), respectively. The study was designed to address long-term (whole season), local processes in a stream i.e. not replicated with respect to streams, although we are fully aware that caution should be taken at pseudoreplication, i.e. when no true replicates are taken (Hurlbert, 1984).

We collected and planted the macrophytes on the 20th June, 2013. *M. spicatum* shoots were collected from the experimental stream, growing at similar flow velocity and substrate. Twelve shoots, each having one apical meristem (100 mm long without any lateral shoots or meristems), were cut from several mother plants. We placed one shoot in each pot filled with sand and to prevent erosion we covered the sand surface with stones (size 5–7 mm). Six pots, each containing one shoot, were placed at the stream bed at both stream flows. In order to exclude the effect of the substrate, we used sediment from the same site in all pots (Lake Krankesjön southern Sweden). This ensured that all shoots received the same amount of nutrients from the sediment and grew in the same type of substrate. The average shoot lengths above sediment were 4.91 (SD, 0.91) and 4.58 (SD, 0.49) cm at high and low stream flow, respectively.

At the end of experiment, each plant was cut at the base and carefully collected in a plastic bag without losing the periphytic algae and invertebrates residing on it. In the laboratory each plant was gently shaken in water to separate periphyton (Zimba and Hopson, 1997) and invertebrates from the macrophytes. Care was taken not to damage the plant shoot and leaves while separating the invertebrates and algae. The invertebrates were stored in 70% ethanol and later determined to genus. Finally, the remaining water sample was filtered through GFC filter and chlorophyll *a* (Chl *a*) was analyzed according to Jespersen and Christofferson (1987).

The length of the main and lateral shoots was measured for each plant and the growth was calculated as:

Length increase (main shoot) = final length of main shoot – initial length above sediment.

Length increase (lateral shoots) = final total length of lateral shoots – initial total length of lateral shoots.

The number of lateral shoots and the degree of branching of each plant was assessed at the end of the experiment. The degree of branching was measured according to Garbey et al. (2004). The categories are '1' no branching, '2' secondary shoot occurred, '3' tertiary shoot grew and so on.

The number of leaf whorls and the distance between the internodes were assessed by counting the number of leaf whorls on the main shoot at the end of the experiment. After deducting the initial length of the main shoot, the number was counted from bottom to 30 mm from the shoot apex. Moreover, the average distance among the internodes was measured in the same way.

The first three whorls below 50 mm from the apex of the main shoot were selected for assessment of leaf whorl area (cm²) of each plant. Each leaf whorl was pictured and leaf whorl area was measured by using ImageJ version 1.46 R (Freely available at <http://rsb.info.nih.gov/ij/download.html>). The stem diameter of the main shoot of each plant was measured at the bottom (where plant was cut at the sediment surface), middle and at 20 mm below the apex. Roots from each pot were carefully rinsed with water to remove the sand particles. Finally, the root and shoot parts were dried separately in 60 °C for 48 h and biomass of each plant was assessed for both plant parts.

Different plant traits were analyzed with regard to different stream flows. One-way ANOVA was used to test the significance of the effects of different stream flows on different plant traits. Data transformation (Log 10) was done if necessary to gain the normal distribution and equal variance. Where assumption of equal variance was not met, Mann–Whitney *U* test was performed instead of one-way ANOVA. The amount of periphyton grown on macrophytes was also analyzed with Mann–Whitney *U* test. All the statistical analysis was done with IBM SPSS Statistics 20.

3. Results and discussion

All the *M. spicatum* shoots were grown in the experimental stream for 78 days starting from 20th June, 2013 to 6th September, 2013. All the six shoots at high stream flow (0.20 m s⁻¹) survived until the end of the experiment and five shoots survived at low stream flow (0.04 m s⁻¹). We observed that the *M. spicatum* shoots at high velocity bent over and gained streamlined morphology, whereas shoots at slow flow made an angle to the substratum and only the apical point of the shoot reached the water surface. The streamlined morphology at high velocity helps the plant to reduce drag force since plant bending toward the substratum and forming shield canopy only face high velocities at the upper surface and experience lower drag force (Sand-Jensen, 2003). The average increase of the main shoot of *M. spicatum* was 35.40 (SD, 26.36) cm and 25.46 (SD, 3.39) cm at low and high flow, respectively ($U = 12.50$, $p = 0.699$, Mann–Whitney *U*-test). The main shoot of one plant at slow flow broke during the experimental growth that caused high standard deviation. Similarly, we found no significant effect of stream flow on the length of total lateral shoots, although the mean length tended to be higher at high than at low flow (107.65 (SD, 81.44), and 21.08 (SD, 39.08) cm, respectively), whereas the opposite trend was observed for main shoot growth (Fig. 1A). Hence, in contrast to our first hypothesis, we found no difference in the length of main or lateral shoots between high and low flows. Boeger and Poulson (2003) found similar results with respect to stem length in *Veronica anagallis-aquatica* L.

The root system is important for the anchorage strength of submerged macrophytes (Fox, 1996), and, accordingly, the root

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