



# The role of patch size in ecosystem engineering capacity: a case study of aquatic vegetation

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## Abstract

Submerged aquatic plants are ecosystem engineers that are able to modify their habitat. However, the role of patch size in the engineering capacity of aquatic plants has not yet been fully investigated, while it could be essential for elucidating the consequences of plant presence. Our objectives were to investigate the effects of patch size on plant-flow-sediment interactions in lotic ecosystems and to determine whether these effects differed according to environmental characteristics. We performed in situ measurements of velocity and grain size along natural patches of increasing length ( $L$ ) at two sites presenting different flow and sediment characteristics. Our results indicated that a minimum patch size was needed to induce in-patch reduction of the time averaged velocity component in the flow direction (i.e. streamwise velocity) and fine sediment accumulation. Streamwise velocity decreased linearly with  $L$  independently of the site conditions. The sediment texture was instead dependent on site conditions: for the site characterized by higher velocity and coarser sediment, the sediment grain size exponentially decreased with  $L$ , reaching a minimum value at  $L \geq 1.0$  m, while for the site characterized by lower velocity and finer sediment, it reached a minimum value already at  $L > 0.3$  m. This study demonstrated that a minimal patch size is required to trigger the ecosystem engineering capacity of aquatic plant patches in lotic environments and that this capacity increases with patch length. Small patches induce little to no modification of the physical habitat, with possible negative feedbacks for plants. With increasing patch size, the habitat modifications induced by plants become more important, potentially triggering positive feedbacks for plants.

**Keywords** Aquatic plants · Patch dynamics · Feedbacks · Hydrodynamics · Sediment dynamics

## Introduction

Rooted submerged aquatic plants are fundamental components of lotic freshwater ecosystems. These primary producers contribute to the functioning of the ecosystem, regulating nutrient cycles, increasing habitat heterogeneity and serving as shelter and habitat for other organisms (Carpenter and Lodge 1986; Cornacchia et al. 2019). As ecosystem engineers (*sensu* Jones et al. 1994), they play an essential role in aquatic ecosystems: rooted submerged plants modify flow conditions and sedimentation patterns (Sand-Jensen 1998; Sand-Jensen and Pedersen 1999), and some species are able to release oxygen into the substrate through their roots, influencing the availability of nutrients and microbial activity and hence biogeochemical processes in the substrate (Cafrey and Kemp 1992; Sand-Jensen et al. 1982; Soana and Bartoli 2013).

In streams, aquatic plants commonly form mono-specific patches (Sand-Jensen and Madsen 1992). The formation of

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patches is due to clonal growth, occurring mainly in the downstream direction (Puijalon et al. 2008; Sand-Jensen and Madsen 1992). In addition to light and nutrient availability, patch expansion also depends on flow conditions and sediment characteristics, as well as the frequency and intensity of flood events, which may contribute to plant and patch uprooting (Bornette and Puijalon 2010; Franklin et al. 2008). Simultaneously, aquatic plant patches modify the flow of running water habitats, which in turn modifies sediment patterns and characteristics.

Patches represent a region of high flow resistance, which causes the flow to deflect and accelerate above and/or next to the canopy, locally increasing water velocity and turbulence at the edges of the patch (Sand-Jensen and Mebus 1996; Sand-Jensen and Pedersen 2008). Because the patches are porous, some flow can pass through the patch, but with a reduced velocity relative to the upstream (Fonseca et al. 1982; Sand-Jensen and Mebus 1996; Sand-Jensen and Pedersen 2008; Vandenbruwaene et al. 2011). The processes of flow deflection away from the patch and flow deceleration within the patch occur over an adjustment length,  $X_D$ , at the leading edge of the patch, which can range from 10 cm to several metres depending on the stem density and geometry of the patch (Chen et al. 2013). Beyond this adjustment length, the velocity, shear stress and turbulence are generally reduced inside plant patches (James et al. 2004; Sand-Jensen and Pedersen 1999; Souliotis and Prinos 2011), leading to a reduced potential for resuspension and erosion (Hendriks et al. 2009). Moreover, because turbulent diffusion is needed to keep particles in suspension, the reduction of turbulence inside plant patches also favours sedimentation (Hendriks et al. 2009; Sand-Jensen 1998; Schulz et al. 2003). As a result of the processes above, sediment tends to accumulate inside plant patches, with an increased proportion of fine particles compared to bare areas, where flow acceleration next to the patch contributes to particle resuspension and erosion (Donatelli et al. 2018; Ganthy et al. 2013; Sand-Jensen 1998; Schoelynck et al. 2013). The plant-induced modifications of the physical environment trigger positive feedbacks for the plants themselves: as the hydrodynamic stress is reduced, the risk of mechanical damage and uprooting is also minimized, while the sediment, enriched in silt particles, enhances the availability of nutrients for plants. As a consequence, plant growth and thus patch expansion are enhanced.

The ecosystem engineering capacity of aquatic plants to modify flow conditions and to influence sediment particle deposition and erosion depends on plant morphology, e.g., flexibility and stem density (Bouma et al. 2009; Sand-Jensen 1998) but also on patch geometry, such as its length, width and height relative to water depth (Nepf 2012). Patch geometry influences flow velocity both inside (Sand-Jensen 1997; Schoelynck et al. 2014) and outside patches (Sand-Jensen

and Mebus 1996; Sand-Jensen and Pedersen 2008), therefore also influencing sedimentation and the accumulation of organic matter (Schoelynck et al. 2012). For instance, for *Callitriche platycarpa*, a freshwater species, the acceleration next to the patch has been negatively related to the canopy depth of submergence and positively to the length/width ratio (Schoelynck et al. 2013), and wider patches present enhanced turbulence downstream of the patch compared to narrower, more streamlined ones (Sand-Jensen and Mebus 1996; Sand-Jensen and Pedersen 2008). For *Spartina alterniflora*, a salt marshes species, velocity reduction and substrate stabilization at the rear of the patch have been demonstrated to be positively related to patch size (Bruno and Kennedy 2000).

Some studies have shown that modifications of flow and sedimentation induced by plant patches depend not only on plant morphology and patch structure but also on hydrodynamic forcing (Bouma et al. 2009; van Wesenbeeck et al. 2008). Specifically, these studies showed that the flow acceleration and erosion adjacent to the patches are negligible under low water velocity and become more important with increasing water velocity. At the same time, another study demonstrated very similar flow patterns for similar patches exposed to different water velocities (Sand-Jensen and Pedersen 1999). These contradictory results indicate that the influence of flow velocity on the modification of flow and deposition by plant patches is still unclear. More importantly, the effect of some key abiotic (i.e., sediment physico-chemical characteristics) and biotic (i.e., patch size) parameters on these processes and their consequences for patch dynamics have not yet been fully investigated.

Plant patch dynamics and their effects on ecological processes across longitudinal, lateral and temporal gradients are still little studied in lotic ecosystems (Winemiller et al. 2010). Investigating plant patches of increasing size can elucidate patch dynamics through time, as increased patch size corresponds to increased age. In streams, patches occur at a wide range of sizes. Sand-Jensen (1998) and Schoelynck et al. (2012) reported many patches of intermediate size (1–2 m long) and fewer patches of other sizes, for *Callitriche* spp. and other aquatic species in lowland streams. This size distribution of natural patches is still unexplained, as well as the modification of the physical forcing to which they are exposed. However, most of the previous studies examining the effect of patch size on associated processes considered intermediate-sized patches, with a length from 1 to 2 m (Sand-Jensen and Pedersen 1999; Schoelynck et al. 2013), which prevents identifying thresholds or shifts occurring at smaller or larger patch sizes. In particular, it is still unknown what minimum size threshold is needed to induce sufficient changes in flow and sedimentation to create positive feedback within the river channel patches, as demonstrated for circular patches in salt marsh environments (Bouma et al. 2007; Bruno and Kennedy

2000). Similarly, the factors that may set the upper size limit for aquatic plant patches in streams are still unknown.

Flume experiments with rigid mimics demonstrated that the deceleration of flow within a patch occurs over an adjustment length, which is related to plant morphology and patch structure (Chen et al. 2013). If the patch length is smaller than the adjustment length, the velocity declines over the entire patch length; alternatively, if the patch length is longer than the adjustment length, the flow has fully adjusted to the patch over the adjustment length, and longer patches do not decrease the velocity further. No studies have investigated whether there is a minimal and a maximal patch size for natural river vegetation or whether, in particular, in-patch sediment processes (e.g., in-patch accumulation of fine sediment) depend on a size threshold. In addition, the role of different site conditions (flow velocity, sediment characteristics) on the effect of patch size on flow and sediment modifications is still not clear. The objectives of the present study were therefore to investigate the effects of patch size on plant-flow-sediment interactions associated with natural vegetation patches in lotic ecosystems and to determine to what extent these effects vary with environmental characteristics. The first hypothesis is that patches of submerged plants in streams have an effect on the habitat (flow and sediment characteristics) that is dependent on patch size. Specifically, a minimum patch size is necessary to induce modification of the flow and sediment characteristics. Further, for patches shorter than the adjustment length, flow decreases exponentially with patch length, but for patches longer than the adjustment length, no further modifications of flow are observable at increasing patch lengths. As sediment texture is positively related with near-bed flow velocity (Sand-Jensen 1998), we expect that the sediment characteristics inside the patch are also dependent on the adjustment length scale, with the same pattern as flow. The second hypothesis is that the patch size thresholds vary between sites, and in particular as a function of water velocity and sediment characteristics: in a channel with higher velocity and coarser sediment, a greater patch length is needed to reduce the velocity to below the deposition threshold.

To test these hypotheses, we performed in situ measurements of velocity and grain size along natural patches of *Callitriche platycarpa*, considering patches of increasing length at two different sites. These sites differ in mean flow velocity and sediment grain size and hence assess the consistency of the processes across different site conditions.

## Materials and methods

### Study sites and species

The study was conducted in two drainage channels of the Upper Rhône River (France), near Brégnier-Cordon

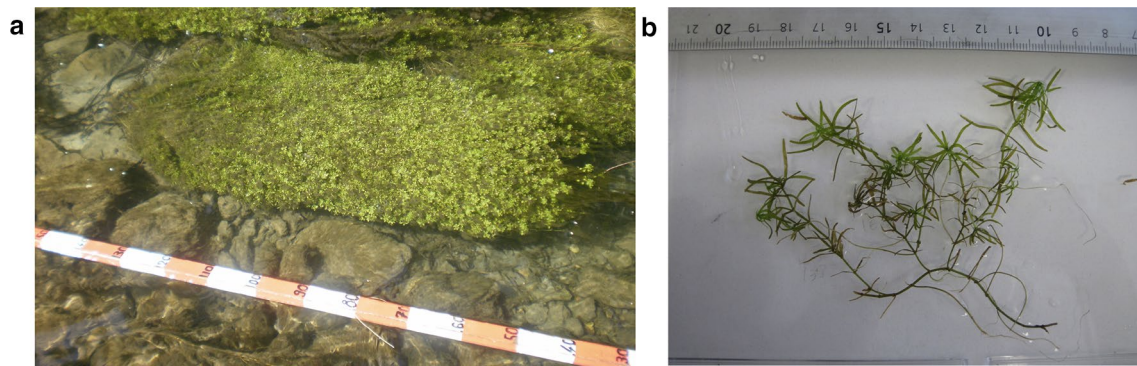
(45.6452 N, 5.6080 E) and Serrières-de-Briord (45.8153 N, 5.4269 E). These artificial drainage channels were selected because they present a more uniform structure (cross-section, water depth, low sinuosity) than natural channels while being naturally colonized by submerged aquatic vegetation. These channels are fed by Rhône river seepage and hillslope aquifers. The type of channel feeding and their management keep the channel discharge particularly stable, especially in spring and summer season. Cover by aquatic vegetation depends on channel section and the season, ranging from 30 to 90% during the winter and summer respectively.

The two sites presented different mean velocities and sediment textures. In the 11 sampling days, depth-average and time-average velocities were higher in Serrières-de-Briord than in Brégnier-Cordon ( $0.20 \pm 0.01 \text{ ms}^{-1}$  and  $0.13 \pm 0.01 \text{ ms}^{-1}$ , respectively, t-test,  $t_{11} = 8.47$ ,  $p < 10^{-4}$ ). The names of the two sites were then abbreviated to HV for the high-velocity site (Serrières-de-Briord) and to LV for the low-velocity site (Brégnier-Cordon). Bare sediments in the channels consisted mainly of medium sand for HV and fine sand for LV (Online Resource 1), following the Wentworth size classes (Wentworth 1922). The fine fraction of the bare sediments upstream of the vegetated patches, represented by the mean of the percentile value  $d_{0.3}$  (see *Sediment characterization*), was significantly higher in HV than in LV over the 11 sampling dates ( $123 \pm 29 \mu\text{m}$  and  $78 \pm 26 \mu\text{m}$ , respectively; t-test,  $t_{11} = -2.88$ ,  $p < 0.01$ ).

The aquatic plant species *Callitriche platycarpa* was studied, as it is abundant in these channels and forms defined patches that are often well isolated (Fig. 1a). At the shoot apex, leaves are densely packed, forming a rosette, which results in a large part of the biomass being concentrated in the upper part of the canopy (Sand-Jensen and Mebus 1996). *C. platycarpa* has thin, flexible and highly branched stems that can be 10–200 cm long (Fig. 1b), forming dense patches due to the entanglement of stems (Tison and de Foucault 2014). Patches of *C. platycarpa* usually present an elliptical structure, and the patch height increases along the patch length. Long patches (usually over 1 m long) present an over-hanging canopy, created by the long, flexible and buoyant stems extending in the downstream direction. Consequently, long patches are rooted only in the upstream part (Fig. 1a).

### Field sampling

During summer 2014, at the peak of the growing season, six patches of *C. platycarpa* were selected at each site. The selected patches were located as far as possible from the channel banks and from other patches to avoid interference. The six patches per site were selected to have increasing length, between 0.16 m and 3.13 m for the LV site and between 0.3 m and 2.5 m for the HV site (Table 1). As patch



**Fig. 1** Patch structure and morphology of *C. platycarpa*: **a** a long patch of *C. platycarpa*, with a typical elliptic shape and an overhanging canopy and only the upstream part of the patch being anchored to

the sediment; **b** young plants of *C. platycarpa*, connected by a runner. Plants are highly branched and present an apex rosette

length ( $L$ ), width ( $W$ ) and maximum height ( $h$ ) were correlated (log–log relationship between  $L$  and  $W$ ,  $r = 0.84$ ,  $p < 10^{-4}$ , and linear relationship between  $L$  and  $h$ ,  $r = 0.83$ ,  $p < 10^{-4}$ ),  $L$  was chosen to describe patch size.  $L/W$ ,  $L/h$  and  $H/h$  ratios (with  $H$ : water depth) are reported in Table 1.

For each patch, coupled measurements of hydrodynamics and collection of sediment samples were performed at six sampling points along its longitudinal axis (two outside and four inside the patch). The two sampling points outside the patch were located approximately 1 m upstream from its leading edge (U) and 1 m downstream from its rear edge (D). The four sampling points inside the patch were located at 10%, 30%, 50%, and 90% of the canopy length, starting from the leading edge. For each position, the velocity profile was measured, and a core of sediment was collected (5 cm diameter and 10 cm deep).

### Hydrodynamic measurements and velocity profiles

Vertical profiles of velocity were measured using a 3D Acoustic Doppler Velocimeter (ADV, FlowTracker Handheld-ADV, SonTek, USA). Vertical profiles were made with depth intervals of less than 12 cm, reduced to 1–4 cm near

plant–water interfaces. Due to the dimensions of the side-looking probe, measurements closest to the sediment were taken at a minimum of 4 cm above the channel bed. Velocity was recorded over 100 s at 1 Hz. Data were filtered to remove spikes (Goring and Nikora 2002; Mori et al. 2007). The time average (denoted by an over bar) of the streamwise (i.e. in the flow direction) velocity component,  $\bar{u}$ , was used to quantify the flow modification induced by plant patches. From each time-averaged velocity profile, the velocity at 20 cm above the bed,  $\bar{u}_{20}$ , was estimated by interpolation. This distance was chosen to avoid bottom interference due to the presence of boulders and cobbles. Moreover, this choice allowed us to measure hydrodynamic forces faced by plants during their growth and the patch development in relation to the patch architecture. Please note that due to the plant morphology and patch architecture (i.e., flexibility of stems, patch height that increases along the patch, and  $L/h$  ratio), measurements at 20 cm of depth were located above the canopy for the smallest patches and at the upstream end of long patches. In these cases,  $\bar{u}_{20}$  may qualitatively capture changes in the velocity field due to lateral deflection of flow away from the patch, but they will definitely over-estimate the velocity within the canopy. Turbulence intensity was not

**Table 1** Characteristics of *C. platycarpa* patches measured at sites HV and LV: length ( $L$ ), width ( $W$ ), maximum height ( $h$ ),  $L/W$  and  $L/h$  ratios of patches, the water depth ( $H$ ) and the depth of submergence ratio ( $H/h$ )

Site	HV						LV					
	Patch n.: 1	2	3	4	5	6	1	2	3	4	5	6
$L$ (m)	0.30	0.65	0.85	1.45	1.90	2.50	0.16	0.33	0.90	1.60	2.27	3.13
$W$ (m)	0.10	0.19	0.55	1.00	0.84	0.66	0.08	0.16	0.50	0.40	0.80	0.70
$h$ (m)	0.02	0.15	0.24	0.29	0.46	0.29	0.03	0.09	0.10	0.20	0.40	0.60
$L/W$	3	3.4	1.5	1.4	2.3	3.8	2	2.1	1.8	4	2.8	4.5
$L/h$	15	4.3	3.5	5	4.1	8.6	5.3	3.6	9	8	5.7	5.2
$H$ (m)	0.54	0.57	0.56	0.89	0.86	0.55	0.48	0.69	0.68	0.65	0.51	0.62
$H/h$	27	3.8	2.3	3.1	1.9	1.9	16	7.7	6.8	3.2	1.3	1.0

Measures were taken with a tape measure; however, note that the patch dimension measurements have an uncertainty of a few centimetres due to the continuous movement of the canopy with the current

included in our study: for the smaller patches, velocity measurements within the patch were absent and this impeded the detection of turbulence variation within the patch from the leading edge for different patch lengths.

To examine the effect of a plant patch on flow conditions within the patch, the 95% confidence interval of the  $\bar{u}_{20}$  within the patch was calculated and compared to the  $\bar{u}_{20}$  value measured at the upstream position ( $\bar{u}_{20U}$ ). Then, we calculated the fractional difference between the local velocity,  $\bar{u}_{20}$ , and the velocity upstream of the patch,  $\bar{u}_{20U}$ . That is, for each position (10%, 30%, 50%, 90% and D), we defined  $\Delta\bar{u}_{20} = (\bar{u}_{20} - \bar{u}_{20U}) \times (\bar{u}_{20U})^{-1}$ . To assess whether the effect of patch length on hydrodynamics differs between the two sites, we performed an analysis of covariance (ANCOVA) using  $\bar{u}_{20}$  and  $\Delta\bar{u}_{20}$  at the 50% position as the dependent variable, site as the effect and patch length as a covariate. The interaction term was included in the model and dropped if not significant. For the analysis of the relation of  $\Delta\bar{u}_{20}$  and  $L$ , an outlier point was omitted due to a very low  $\bar{u}_{20U}$  resulting from the interaction with an upstream patch.

### Sediment characterization

After sampling, the collected sediment cores were stored at 4 °C. To perform the effective grain size analyses (i.e. for the whole sediment, without removal of organic matter, McCave and Syvitski 1991; Phillips and Walling 1999), sediments were wet sieved with distilled water at 1.6 mm, separating the fine and the coarse fraction, and then dried at 70 °C for 48 h to allow sample preservation until the analyses were completed. Grain size analyses of sediment were performed in the aqueous phase by laser diffractometry using a Malvern Mastersizer 2000 G (diameter range: 0.01–2000  $\mu\text{m}$ ). The analytical model used is based on the Fraunhofer theory, which assumes spherical particles. Prior to the measurements, sediments were sonicated for 2 min to destroy the aggregated particles formed during the 70 °C drying process (Badin et al. 2009). The results of the analysis are displayed as grain size distribution curves. The mode of the curve indicates the most abundant grain size in terms of the percentage per total solid volume. The curves were transformed into cumulative curves, and the percentile values  $d_{0.1}$ ,  $d_{0.3}$ ,  $d_{0.5}$ , were calculated (maximum diameter corresponding to 10%, 30%, and 50%, respectively, of the total particle volume). The three values were found to be correlated, and only the percentile value  $d_{0.3}$  was kept for further analyses. Measurements of grain size were conducted in triplicate for each sample, and mean values and standard deviations of  $d_{0.3}$  were calculated. To describe the sediment texture at each sampling position, we used only the mean value of  $d_{0.3}$ , as the standard deviation was less than 10%.

To assess the effect of the patch size on the sediment texture within the patch, the 95% confidence interval of the

$d_{0.3}$  within the patch was calculated and compared to the  $d_{0.3}$  value measured at the upstream position ( $d_{0.3U}$ ). Then, for each position (10%, 30%, 50%, 90% and D), we expressed the  $d_{0.3}$  relatively to the  $d_{0.3U}$  to obtain the relative value  $\Delta d_{0.3}$ , as  $\Delta d_{0.3} = (d_{0.3} - d_{0.3U}) \times (d_{0.3U})^{-1}$ . The  $\Delta d_{0.3}$  at the 50% position was used to assess whether the effect of patch length on sediment texture differs between the two sites. As the relationship between  $\Delta d_{0.3}$  at the 50% position and patch length was not linear, we fitted for each site an exponential model following the equation  $\Delta d_{0.3} = a + b^c L$ .

## Results

### Flow velocity

The streamwise velocity profiles upstream of the patches generally followed a typical boundary layer profile. At positions within the patches,  $\bar{u}$  was highest above the canopy, decreased just above the canopy, and usually reaching approximately zero within the canopy (Online Resource 2).

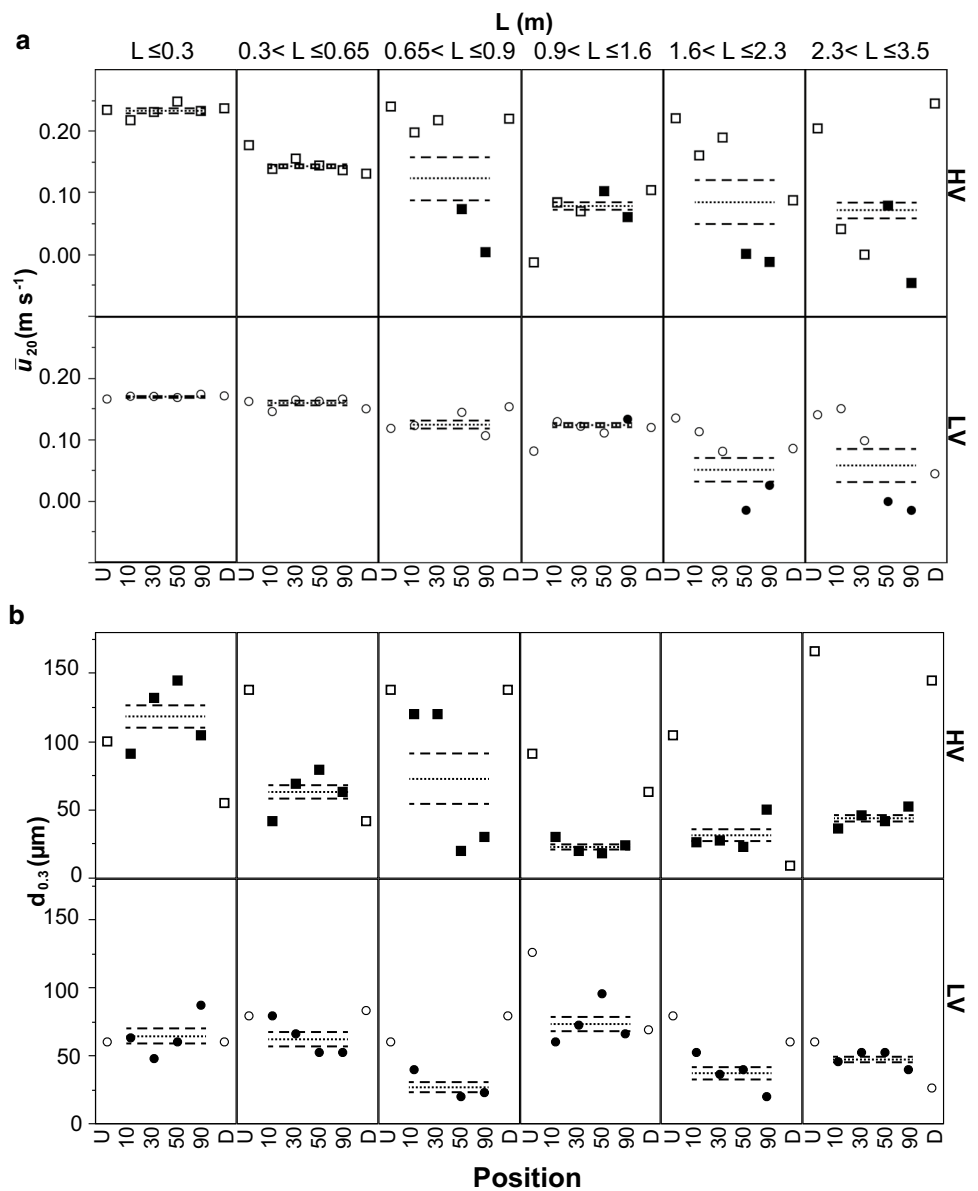
For short patches ( $L \leq 0.3$  m and  $L \leq 0.9$  m for the HV and LV sites, respectively), the  $\bar{u}_{20}$  measured at the upstream position ( $\bar{u}_{20U}$ ) was very close or within the 95% confidence interval of the  $\bar{u}_{20}$  values within the patch (Fig. 2a). For these short patches, the  $\bar{u}_{20}$  was stable along the patch (Fig. 2a), because the measurement of  $\bar{u}_{20}$  was conducted above the canopy. For all the longer patches but 2, the  $\bar{u}_{20U}$  was higher than the 95% confidence interval of the  $\bar{u}_{20}$  values within the patch and the  $\bar{u}_{20}$  values gradually decreased along patches, with velocity close to zero observed at the 90% position in longest patches (Fig. 2a).

For both sites, the average velocity ( $\bar{u}_{20}$ ) at the 50% position decreased linearly with patch length (ANCOVA,  $F_{1,10} = 22.9$ ,  $p < 0.001$ , Fig. 3a), and this relationship was independent from the interaction between site and patch length (ANCOVA,  $F_{3,8} = 0.02$ ,  $p = 0.88$ ) and from site (ANCOVA,  $F_{2,9} = 0.02$ ,  $p = 0.89$ ). Similarly, the relative variation in average velocity ( $\Delta\bar{u}_{20}$ ) at the 50% position decreased linearly with patch length (ANCOVA,  $F_{1,9} = 8.31$ ,  $p < 0.02$ , Fig. 3b), and this relationship was independent from the interaction between site and patch length (ANCOVA,  $F_{3,7} = 0.10$ ,  $p = 0.76$ ) and from site (ANCOVA,  $F_{2,8} = 1.45$ ,  $p = 0.26$ ). In three cases for which the velocity measurement was above the canopy (Fig. 3b, open symbols)  $\Delta\bar{u}_{20}$  was positive, indicating an increase in velocity along the patch, which was likely due to the upward deflection of flow resulting in flow acceleration above the canopy.

### Sediment characteristics

For short patches ( $L \leq 0.3$  m), the  $d_{0.3}$  measured at the upstream position ( $d_{0.3U}$ ) was within or lower than the 95%

**Fig. 2 a** Time-averaged streamwise velocities,  $\bar{u}_{20}$ , and **b** the  $d_{0.3}$  value in the grain size distribution measured at six positions for each patch: upstream (U), along the patch at 10%, 30%, 50% and 90% of its length, and downstream (D) along patches of the species *C. platycarpa* of increasing length ( $L$ ) for the sites HV and LV. Empty symbols (squares for HV and circles for LV) indicate that the data refer to a position outside the patch canopy (either in the position U, D or when canopy was lower than 20 cm for  $\bar{u}_{20}$ ), whereas full symbols indicate data collected inside the patch canopy. The dotted and dashed lines represent the mean and the 95% confidence intervals of the in-patch values



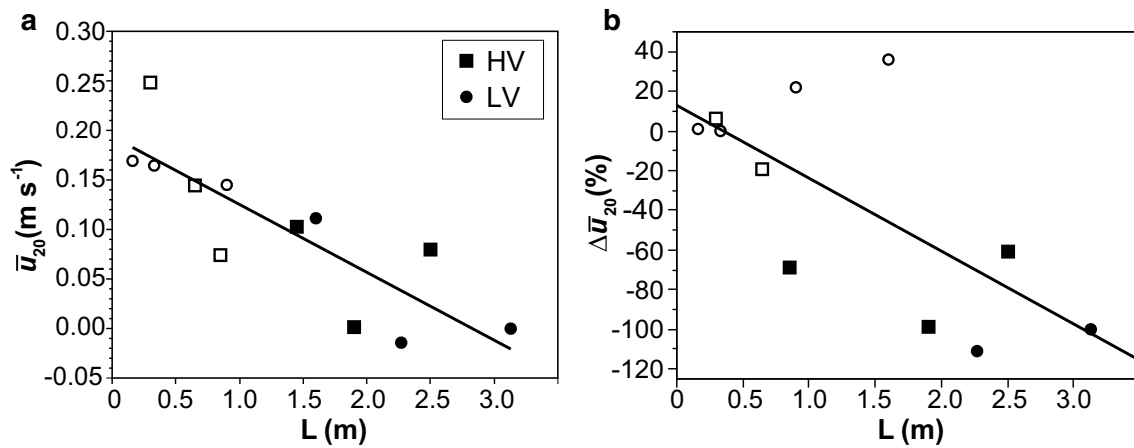
confidence interval of the  $d_{0.3}$  values within the patch, indicating that the in-patch sediment was similar or coarser than at the upstream position. On the contrary, for longer patches ( $L > 0.3$  m), the  $d_{0.3U}$  was always higher than the 95% confidence interval of the  $d_{0.3}$  values within the patch, indicating finer grain size inside patches compared to upstream position (Fig. 2b, Online Resource 3).

The relationship between  $\Delta d_{0.3}$  at the 50% position and patch length was different at the 2 sites. For the HV site, the  $\Delta d_{0.3}$  exponentially decreased with patch length ( $\Delta d_{0.3} = 4.71e^{-4.39L} - 0.80$ ,  $R^2 = 0.96$ ,  $p < 0.05$ ): the  $\Delta d_{0.3}$  decreased with patch length up to patches of 1.0 m, where it reached a threshold value around  $-80\%$  of  $d_{0.3U}$  (Fig. 4), corresponding to  $d_{0.3} = 25 \mu\text{m}$  (data not shown). For the LV site, even though the relationship between  $\Delta d_{0.3}$

and patch length was not significant ( $\Delta d_{0.3} = 2.96 e^{-12.8L} - 0.38$ ,  $R^2 = 0.40$ ,  $p = 0.75$ , Fig. 4), the  $\Delta d_{0.3}$  was reduced by between  $-13$  and  $-67\%$  of the  $d_{0.3U}$  for all the patches with  $L > 0.3$  m, with a mean value of  $-38\%$ , corresponding to  $d_{0.3} = 52 \mu\text{m}$  (data not shown).

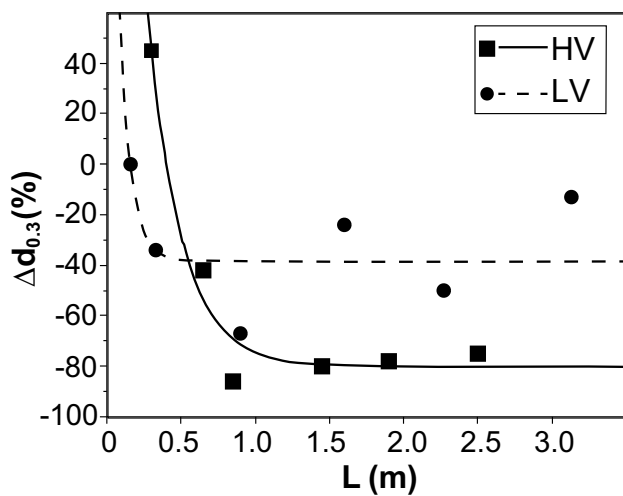
**Effect of patch length on both sediment and flow**

The relationship among relative velocity ( $\Delta \bar{u}_{20}$ ), grain size distribution ( $\Delta d_{0.3}$ ) and patch length can be summarized in a contour plot from the data relative to the 50% position, where the effect of the patch on flow velocity and sediment characteristics is expected to be maximal (Fig. 5). Small patches ( $L < 1.1$  m) may produce an increase in both  $\Delta \bar{u}_{20}$  and  $\Delta d_{0.3}$  (quadrant I of the plot), while for larger patches



**Fig. 3** Effect of patch length on velocity by the freshwater species *C. platycarpa* for the two sites. **a**  $\bar{u}_{20}$  at the 50% position was linearly negatively related to patch length ( $F_{1,10} = 22.9, p < 0.001$ ), without significant differences between sites ( $F_{2,9} = 0.02, p = 0.89$ ). **b**  $\Delta\bar{u}_{20}$  at the 50% position was linearly negatively related to patch length ( $F_{1,9}$

$= 8.31, p < 0.02$ ), without significant differences between sites ( $F_{2,8} = 1.45, p = 0.26$ ). Empty symbols (squares for HV and circles for LV) indicate that the canopy was lower than 20 cm for  $\bar{u}_{20}$ , whereas full symbols indicate data collected inside the patch canopy



**Fig. 4** Effect of patch length on sediment characteristics associated with the species *C. platycarpa* for the two sites.  $\Delta d_{0.3}$  at the 50% position exponentially decreased with patch length ( $R^2 = 0.96, p < 0.05$  for HV and  $R^2 = 0.40, p = 0.75$  for LV), and the relationship was different between the two sites

( $L > 1.1$  m), the increase in patch length generally results in reduction in both  $\Delta\bar{u}_{20}$  and  $\Delta d_{0.3}$  (quadrant III of the plot).

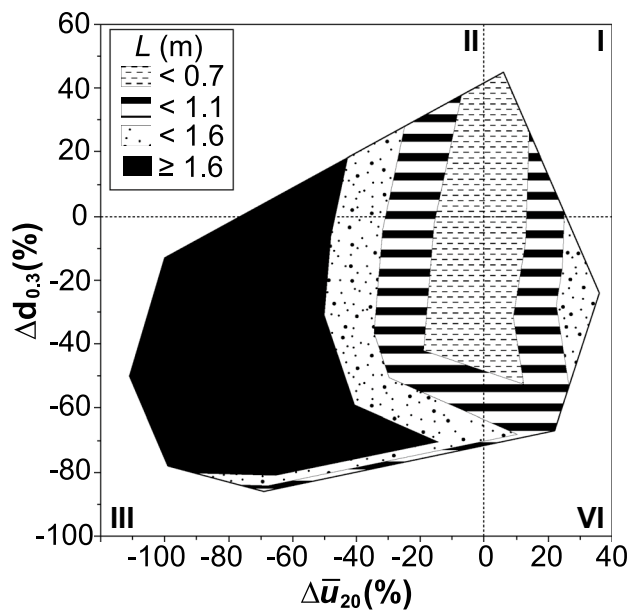
### Discussion

Patch structural characteristics are important factors that determine the capacity of a species to influence flow and sedimentation processes. The present study investigated the effects of patch size on these processes in order to test

whether the effect of submerged plant patches on flow and sediment texture is dependent on patch size and whether this effect differs according to environmental conditions. Our results indicated that a minimal patch size is required to induce modifications of flow and sediment characteristics ( $L > 0.3$  m and  $L > 0.9$  m for the HV and LV sites, respectively for the flow, and  $L > 0.3$  m for the sediment characteristics). Moreover, streamwise velocity decreased linearly with patch length independently of the site conditions (Fig. 3). However, the sediment texture was dependent on site conditions (Fig. 4): for the HV site, the  $\Delta d_{0.3}$  in the middle of the patch exponentially decreased with patch length, reaching a minimum value at  $L \geq 1.0$  m, while for the LV site, the  $\Delta d_{0.3}$  decreased for all the patches with  $L > 0.3$  m.

### Effect of patch length on flow reduction

Our results demonstrate that submerged aquatic patches generally exhibited reduced in-patch velocity, as previously shown (Sand-Jensen 1998; Sand-Jensen and Pedersen 1999). In accordance with our first hypothesis, we demonstrated, for the first time in the field, that modifications of velocity depend on patch size, and importantly, that a minimum patch size is needed to induce modification of the flow (Fig. 3). The velocity near the patch was reduced to a greater degree by long patches, and for longer patches ( $L > 0.3$  m and  $L > 0.9$  m for the HV and LV sites, respectively), the velocity tended to be reduced from upstream to downstream to values close to 0 or even negative in the downstream part of the patch, which is consistent with previous results (Schoelynck et al. 2013). Negative values were associated with the vertical shear and recirculation generated in the



**Fig. 5** Contour plot of the effect of patch length on both velocity ( $\Delta\bar{u}_{20}$ ) and sediment texture ( $\Delta d_{0.3}$ ) at both sites measured in the centre of the patches (50% position). The contour plot describes how the ecosystem engineer capacity of aquatic plant patches increases with patch length. Small patches induce little to no modification of the physical habitat, with possible negative feedback (e.g., increased grain size related to increased turbulence at the leading edge, quadrant I). With increasing patch size, habitat modification (i.e., reduction of velocity and reduced sediment texture) became more important (quadrant III) and should induce positive feedbacks for plants. Please note that (1) quadrant II is an artefact of the contour plot as, physically, a reduction in water velocity will always lead to a reduction in sediment texture and never to an increase in it (indeed, none of the patches measured was included in this quadrant); (2) quadrant IV results from our methodological approach (streamwise velocity measured at 20 cm) that, for small patches ( $L < 1.1$  m), detects the velocity acceleration above the patch ( $\Delta\bar{u}_{20} > 0$ ) and not the velocity reduction inside the canopy, with the latter inducing the reduction of the sediment texture ( $\Delta d_{0.3} < 0$ )

wake of the patch, e.g., details of which are illustrated in Fig. 2 of Folkard (2005).

Velocity linearly decreased with increasing patch length, although we caution that in-patch velocities were only available for the longest patches ( $L > 1.1$  m), and this conclusion is limited to our data that are relative to a depth of 20 cm, as other measurements below this depth should result in lower velocities. Indeed, for certain patches ( $L < 1.1$  m), the majority of velocity measurements were taken above the patch. For small patches ( $L < 0.65$  m),  $\Delta\bar{u}_{20}$  was equal to zero, indicating that the patch had little influence on velocity at the measured depth, while for certain intermediate patches ( $0.65 \text{ m} < L < 1.6$  m),  $\Delta\bar{u}_{20}$  had positive values, so this parameter described the acceleration of flow above the canopy, and it is an over-estimate of the in-patch velocity.

The absence of an adjustment length (i.e., an exponential reduction of the streamwise velocity up to a distance

from the leading edge over which no further modification of flow is observable) in our data may indicate that the adjustment length was longer than the patch length in all cases due to the patch architecture of *C. platycarpa*, characterized by a very dense, flexible overhanging canopy and a positive correlation between patch height and length, which may lead to a different flow pattern than patches with different architecture (Chen et al. 2013). In addition, the positive relationship between patch height and length implies that the submergence ratio ( $H/h$ ) varies with patch length: very small patches ( $L \leq 0.3$  m) are deeply submerged ( $H/h > 10$ ; Table 1), whereas, for increasing length, patches become shallow submerged or even emergent, i.e. the canopy reaches the water surface ( $H/h$  gradually decreases for increasing length, until values close to 1, Table 1). The longest patches of *C. platycarpa* present a gradual decrease of the ratio  $H/h$  from upstream to downstream, due to the flexibility and buoyancy of the canopy. As the  $H/h$  ratio controls the relative importance of the turbulent stress at the top of the canopy and the pressure gradient of the flow (Nepf 2012), the variation of  $H/h$  with patch length may consequently have an important role in flow and sedimentation patterns for different patch length that deserves further investigations.

Contrary to our second hypothesis, despite differences in flow conditions between the two sites, no difference could be observed in the effect of patch length on flow reduction between the two sites, indicating that patch length had similar effects on flow reduction even under slightly different environmental conditions. Our results are consistent with those from previous studies that showed very similar flow velocities in patches of the same species in different streams (Sand-Jensen and Pedersen 1999).

The capacity to modify the surrounding physical environment is a species-specific property that depends on plant traits (Bouma et al. 2010; Sand-Jensen and Pedersen 1999). Plant morphology and canopy architecture are important factors that determine the capacity of a species to modify flow characteristics (Fonseca and Fisher 1986; Sand-Jensen 1998; Schoelynck et al. 2014). A comparison of stiff and flexible species in salt marshes demonstrated how the stiff species was the most efficient ecosystem engineer, where ecosystem engineer efficiency is defined as the benefit–cost ratio per unit of biomass investment. Specifically, stiff species are able to attenuate the wave energy with a slightly lower drag force per unit biomass (Bouma et al. 2010). Future studies may focus on lotic species with contrasting canopy architecture and patch structure in order to test whether they present different patterns of flow reduction with increasing patch length.



## Effect of patch length on sediment texture

As previously demonstrated, we observed the accumulation of fine sediment within plant patches (Sand-Jensen 1998; Schoelynck et al. 2013). In accordance with our first hypothesis, we demonstrated that the grain size within patches depends on patch size: small patches showed similar or coarser sediment compared to upstream conditions, and a minimum patch length was necessary for fine sediment accumulation that reduced the average grain size. At both sites, very short patches ( $L \leq 0.3$  m) presented erosion or no effect on the sedimentation processes, as already observed in salt marsh environments for circular patches (Bouma et al. 2007). The increased grain size observed for short patches may be related to increased turbulence at the leading edge, resulting in enhanced erosion of fine particles. This process has been observed both in the field for submerged vegetation in streams (Cotton et al. 2006) and in laboratory studies with plant mimics (Zong and Nepf 2010, 2011). Above a minimal size ( $L > 0.3$  m), finer sediment accumulation was observed. The reduction of velocity and turbulence within a patch favours the sedimentation of smaller particles (Hendriks et al. 2009; Liu and Nepf 2016; Sand-Jensen 1998; Schulz et al. 2003). In addition, suspended and bed-transported particles may be retained inside plant patches by collision with stems and leaves (Hendriks et al. 2008; Pluntke and Kozerski 2003). We demonstrated that the sediment texture distribution decreased exponentially as a function of patch length for the HV site, indicating that maximum sediment trapping was reached at a short length (approx. 1 m). For the LV site, even though the exponential relationship was not significant, the data suggest that the maximum sediment trapping potential was reached at  $L = 0.33$  m.

In agreement with our first hypothesis, with increasing patch length, the accumulation of fine particles of sediment inside the patch increases up to a threshold length over which patches showed similar sediment texture distribution independently of patch length. This threshold length may correspond to the adjustment length,  $X_D$  (Chen et al. 2013), observed for artificial patches in flume experiments.  $X_D$  is the distance from the leading edge over which the velocity changes inside the patch, which is a function of patch stem density and height. Once the patch length exceeds  $X_D$ , the in-patch velocity does not decrease further with increasing length, and so the grain size does not change with further increases in patch length. In agreement with our second hypothesis, the two sites presented two different thresholds (1 and 0.33 m for HV and LV, respectively) and minimum  $d_{0.3}$  values (25 and 52  $\mu\text{m}$  for HV and LV, respectively). The difference in sediment texture ( $d_{0.3}$  values) can be considered as a fingerprint of the suspended sediment available at the site: sites with lower values (HV) may have finer sediment in suspension and therefore require lower velocities to

deposit all ranges of suspended particle sizes, including the finest ones. Very low flow velocities are found only in long patches, and, therefore, the finest sediments are present only in the long patches (for HV,  $L > 1.0$  m). Reciprocally, sites with a higher  $d_{0.3}$  value (LV) may have suspended particles of larger dimension; in this case, even the finest range of particles available may also tend to deposit at higher near-bed velocities and therefore even in smaller patches (for LV,  $L > 0.33$  m). The differences observed between the two sites may also be due to differences in plant morphology (e.g., stem density), leading to different adjustment lengths (Chen et al. 2013). In this case, a minimum velocity would be reached at different patch lengths, resulting in different sediment deposition patterns. The process of fine sediment accumulation within a patch may thus be influenced by both site conditions and plant and patch characteristics. Moreover, our finding may be influenced by the uniform condition of the sites in which the study was conducted: other sites with more variable conditions (e.g., channel structure, flow temporal variability) may present more complex flow and sedimentation patterns.

## Effect of patch length on both sediment and flow

In accordance with our first hypothesis, we demonstrate that an increase in patch length generally results in a reduction in both  $\Delta \bar{u}_{20}$  and  $\Delta d_{0.3}$  for large patches ( $L > 1.1$  m). For the small patches ( $L < 1.1$  m), the majority of velocity measurements were conducted above the patch; in this case, values of  $\Delta \bar{u}_{20} > 0$  describe the acceleration of flow above the canopy and over-estimate the in-patch velocity. In particular, the IV quadrant of Fig. 5, with  $\Delta \bar{u}_{20} > 0$  and  $\Delta d_{0.3} < 0$ , describes a reduction in the sediment texture that should be related to a reduction in velocity inside the canopy that is not revealed by our measurements, as it occurs at a depth  $< 20$  cm. Indeed, it is physically unlikely that the velocity within the patch was greater than the upstream velocity. However, it is clear that for shorter patches, the sediment texture was, in some cases, coarser than that under upstream conditions, and this modification of the sediment characteristics may be related to increased turbulence at the leading edge (Cotton et al. 2006; Zong and Nepf 2010, 2011).

In conclusion, this study demonstrated that sediment texture and hydrodynamics along patches are strongly dependent on patch length. In particular, a minimal patch size is required to significantly reduce velocity and accumulate fine sediment within plant patches, indicating that the ecosystem engineering effect of *C. platycarpa* is limited or even negative for small patches. A minimal patch size required to trigger the ecosystem engineering capacity of a species was already demonstrated for *S. alterniflora* in salt marsh environments: the habitat modification induced by small patches is not sufficient to facilitate

the establishment of other species in the patch, which is observed in longer patches (Bruno and Kennedy 2000). Similarly, we demonstrated that the engineering effect of *C. platycarpa* increases with increasing patch length, likely as a consequence of the increase in the quantity of plants that intercept flow. The reduced velocity and increased sedimentation occurring within plant patches may lower the risk of plants suffering mechanical damage through the reduction of hydrodynamic forces (Sand-Jensen and Pedersen 2008; Schoelynck et al. 2012) and may increase nutrient availability due to the accumulation of fine sediment and associated nutrients, such as phosphorus (Sand-Jensen 1998). The effects of plant patches on flow and sediment characteristics may thus induce positive feedback for plants, favouring their growth and patch expansion. Future research must thus focus on the effect of patch length on nutrient accumulation and associated biogeochemical processes.

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