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Sara Puijalon

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4 **1 The role of patch size in ecosystem engineering capacity: a case study of aquatic vegetation**

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7 2 Sofia Licci^{1, *}, Heidi Nepf², Cécile Delolme^{1, 3}, Pierre Marmonier¹, Tjeerd J. Bouma⁴, and Sara
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9 3 Puijalon¹

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15 5 ¹Univ Lyon, Université Claude Bernard Lyon 1, CNRS, ENTPE, UMR 5023 LEHNA, F-
16
17 6 69622, Villeurbanne, France

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19
20 7 ²Department of Civil and Environmental Engineering, Massachusetts Institute of Technology,
21
22 8 Cambridge, Massachusetts, USA

23
24
25 9 ³Univ Lyon, INSA-LYON, DEEP, F-69621 Villeurbanne, France

26
27 10 ⁴NIOZ Royal Netherlands Institute for Sea Research, Department of Estuarine and Delta
28
29 11 Systems, P.O. Box 140, 4400 AC Yerseke, The Netherlands

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31
32 12 *correspondence: sofia.licci@univ-lyon1.fr

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36 13 **Keywords:** aquatic plants, patch dynamics, feedbacks, hydrodynamics, sediment dynamics.

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38
39 14 **Abstract**

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42 15 Submerged aquatic plants are ecosystem engineers that are able to modify their habitat. However,
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44 16 the role of patch size in the engineering capacity of aquatic plants has not yet been fully
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46 17 investigated, while it could be essential for elucidating the consequences of plant presence. Our
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48 18 objectives were to investigate the effects of patch size on plant-flow-sediment interactions in lotic
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50 19 ecosystems and to determine whether these effects differed according to environmental
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52 20 characteristics.

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56 21 We performed in situ measurements of velocity and grain size along natural patches of increasing
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58 22 length (L) at two sites presenting different flow and sediment characteristics. Our results

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4 23 indicated that a minimum patch size was needed to induce in-patch reduction of the time
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6 24 averaged velocity component in the flow direction (i.e. streamwise velocity) and fine sediment
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9 25 accumulation. Streamwise velocity decreased linearly with L independently of the site conditions.
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11 26 The sediment texture was instead dependent on site conditions: for the site characterized by
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14 27 higher velocity and coarser sediment, the sediment grain size exponentially decreased with L ,
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16 28 reaching a minimum value at $L \geq 1.0$ m, while for the site characterized by lower velocity and
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19 29 finer sediment, it reached a minimum value already at $L > 0.3$ m. This study demonstrated that a
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21 30 minimal patch size is required to trigger the ecosystem engineering capacity of aquatic plant
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24 31 patches in lotic environments and that this capacity increases with patch length. Small patches
25
26 32 induce little to no modification of the physical habitat, with possible negative feedbacks for
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29 33 plants. With increasing patch size, the habitat modifications induced by plants become more
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31 34 important, potentially triggering positive feedbacks for plants.
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36 **Introduction**

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38 37 Rooted submerged aquatic plants are fundamental components of lotic freshwater
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41 38 ecosystems. These primary producers contribute to the functioning of the ecosystem, regulating
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43 39 nutrient cycles, increasing habitat heterogeneity and serving as shelter and habitat for other
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45 40 organisms (Carpenter and Lodge 1986; Cornacchia et al. 2019). As ecosystem engineers (*sensu*
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48 41 Jones et al.1994), they play an essential role in aquatic ecosystems: rooted submerged plants
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50 42 modify flow conditions and sedimentation patterns (Sand-Jensen 1998; Sand-Jensen and
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53 43 Pedersen 1999), and some species are able to release oxygen into the substrate through their
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55 44 roots, influencing the availability of nutrients and microbial activity and hence biogeochemical
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58 45 processes in the substrate (Caffrey and Kemp 1992; Sand-Jensen et al. 1982; Soana and Bartoli
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60 46 2013).
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4 47 In streams, aquatic plants commonly form mono-specific patches (Sand-Jensen and
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6 48 Madsen 1992). The formation of patches is due to clonal growth, occurring mainly in the
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9 49 downstream direction (Puijalon et al. 2008; Sand-Jensen and Madsen 1992). In addition to light
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11 50 and nutrient availability, patch expansion also depends on flow conditions and sediment
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14 51 characteristics, as well as the frequency and intensity of flood events, which may contribute to
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16 52 plant and patch uprooting (Bornette and Puijalon 2010; Franklin et al. 2008). Simultaneously,
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19 53 aquatic plant patches modify the flow of running water habitats, which in turn modifies sediment
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21 54 patterns and characteristics.

23 55 Patches represent a region of high flow resistance, which causes the flow to deflect and
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26 56 accelerate above and/or next to the canopy, locally increasing water velocity and turbulence at the
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29 57 edges of the patch (Sand-Jensen and Mebus 1996; Sand-Jensen and Pedersen 2008). Because the
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31 58 patches are porous, some flow can pass through the patch, but with a reduced velocity relative to
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34 59 the upstream (Fonseca et al. 1982; Sand-Jensen and Mebus 1996; Sand-Jensen and Pedersen
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36 60 2008; Vandenbruwaene et al. 2011). The processes of flow deflection away from the patch and
37
38 61 flow deceleration within the patch occur over an adjustment length, X_D , at the leading edge of the
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41 62 patch, which can range from 10 cm to several metres depending on the stem density and
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43 63 geometry of the patch (Chen et al. 2013). Beyond this adjustment length, the velocity, shear stress
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46 64 and turbulence are generally reduced inside plant patches (James et al. 2004; Sand-Jensen and
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48 65 Pedersen 1999; Souliotis and Prinos 2011), leading to a reduced potential for resuspension and
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51 66 erosion (Hendriks et al. 2009). Moreover, because turbulent diffusion is needed to keep particles
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53 67 in suspension, the reduction of turbulence inside plant patches also favours sedimentation
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55 68 (Hendriks et al. 2009; Sand-Jensen 1998; Schulz et al. 2003). As a result of the processes above,
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58 69 sediment tends to accumulate inside plant patches, with an increased proportion of fine particles
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60 70 compared to bare areas, where flow acceleration next to the patch contributes to particle

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4 71 resuspension and erosion (Donatelli et al. 2018; Ganthy et al. 2013; Sand-Jensen 1998;
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6 72 Schoelynck et al. 2013). The plant-induced modifications of the physical environment trigger
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8 73 positive feedbacks for the plants themselves: as the hydrodynamic stress is reduced, the risk of
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10 74 mechanical damage and uprooting is also minimized, while the sediment, enriched in silt
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12 75 particles, enhances the availability of nutrients for plants. As a consequence, plant growth and
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14 76 thus patch expansion are enhanced.

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18 77 The ecosystem engineering capacity of aquatic plants to modify flow conditions and to
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20 78 influence sediment particle deposition and erosion depends on plant morphology, *e.g.*, flexibility
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22 79 and stem density (Bouma et al. 2009; Sand-Jensen 1998) but also on patch geometry, such as its
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24 80 length, width and height relative to water depth (Nepf 2012). Patch geometry influences flow
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26 81 velocity both inside (Sand-Jensen 1997; Schoelynck et al. 2014) and outside patches (Sand-
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28 82 Jensen and Mebus 1996; Sand-Jensen and Pedersen 2008), therefore also influencing
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30 83 sedimentation and the accumulation of organic matter (Schoelynck et al. 2012). For instance, for
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32 84 *Callitriche platycarpa*, a freshwater species, the acceleration next to the patch has been
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34 85 negatively related to the canopy depth of submergence and positively to the length/width ratio
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36 86 (Schoelynck et al. 2013), and wider patches present enhanced turbulence downstream of the
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38 87 patch compared to narrower, more streamlined ones (Sand-Jensen and Mebus 1996; Sand-Jensen
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40 88 and Pedersen 2008). For *Spartina alterniflora*, a salt marshes species, velocity reduction and
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42 89 substrate stabilization at the rear of the patch have been demonstrated to be positively related to
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44 90 patch size (Bruno and Kennedy 2000).

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48 91 Some studies have shown that modifications of flow and sedimentation induced by plant
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50 92 patches depend not only on plant morphology and patch structure but also on hydrodynamic
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52 93 forcing (Bouma et al. 2009; van Wesenbeeck et al. 2008). Specifically, these studies showed that
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54 94 the flow acceleration and erosion adjacent to the patches are negligible under low water velocity

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95 and become more important with increasing water velocity. At the same time, another study
96 demonstrated very similar flow patterns for similar patches exposed to different water velocities
97 (Sand-Jensen and Pedersen 1999). These contradictory results indicate that the influence of flow
98 velocity on the modification of flow and deposition by plant patches is still unclear. More
99 importantly, the effect of some key abiotic (*i.e.*, sediment physico-chemical characteristics) and
100 biotic (*i.e.*, patch size) parameters on these processes and their consequences for patch dynamics
101 have not yet been fully investigated.

102 Plant patch dynamics and their effects on ecological processes across longitudinal, lateral
103 and temporal gradients are still little studied in lotic ecosystems (Winemiller et al. 2010).

104 Investigating plant patches of increasing size can elucidate patch dynamics through time, as
105 increased patch size corresponds to increased age. In streams, patches occur at a wide range of
106 sizes. Sand-Jensen (1998) and Schoelynck et al. (2012) reported many patches of intermediate
107 size (1-2 m long) and fewer patches of other sizes, for *Callitriche* spp. and other aquatic species
108 in lowland streams. This size distribution of natural patches is still unexplained, as well as the
109 modification of the physical forcing to which they are exposed. However, most of the previous
110 studies examining the effect of patch size on associated processes considered intermediate-sized
111 patches, with a length from 1 to 2 m (Sand-Jensen and Pedersen 1999; Schoelynck et al. 2013),
112 which prevents identifying thresholds or shifts occurring at smaller or larger patch sizes. In
113 particular, it is still unknown what minimum size threshold is needed to induce sufficient changes
114 in flow and sedimentation to create positive feedback within the river channel patches, as
115 demonstrated for circular patches in salt marsh environments (Bouma et al. 2007; Bruno and
116 Kennedy 2000). Similarly, the factors that may set the upper size limit for aquatic plant patches
117 in streams are still unknown.

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

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

146
147 **Materials and methods**

148 *Study sites and species*

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

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

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4 166 *characterization*), was significantly higher in HV than in LV over the 11 sampling dates
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6 167 ($123\pm 29\mu\text{m}$ and $78\pm 26\mu\text{m}$, respectively; t-test, $t_{11}=-2.88$, $p<0.01$).
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9 168 The aquatic plant species *Callitriche platycarpa* was studied, as it is abundant in these
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11 169 channels and forms defined patches that are often well isolated (Fig. 1a). At the shoot apex,
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14 170 leaves are densely packed, forming a rosette, which results in a large part of the biomass being
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16 171 concentrated in the upper part of the canopy (Sand-Jensen and Mebus 1996). *C. platycarpa* has
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19 172 thin, flexible and highly branched stems that can be 10-200cm long (Fig. 1b), forming dense
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21 173 patches due to the entanglement of stems (Tison and de Foucault 2014). Patches of *C. platycarpa*
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24 174 usually present an elliptical structure, and the patch height increases along the patch length. Long
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26 175 patches (usually over 1 m long) present an over-hanging canopy, created by the long, flexible and
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29 176 buoyant stems extending in the downstream direction. Consequently, long patches are rooted
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31 177 only in the upstream part (Fig. 1a).
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34 35 36 179 *Field sampling*

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38 180 During summer 2014, at the peak of the growing season, six patches of *C. platycarpa*
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41 181 were selected at each site. The selected patches were located as far as possible from the channel
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43 182 banks and from other patches to avoid interference. The six patches per site were selected to have
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46 183 increasing length, between 0.16 m and 3.13 m for the LV site and between 0.3 m and 2.5 m for
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48 184 the HV site (Table 1). As patch length (L), width (W) and maximum height (h) were correlated
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51 185 (log-log relationship between L and W , $r = 0.84$, $p < 10^{-4}$, and linear relationship between L and
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53 186 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
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55 187 depth) are reported in Table 1.
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58 188 For each patch, coupled measurements of hydrodynamics and collection of sediment
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60 189 samples were performed at six sampling points along its longitudinal axis (two outside and four
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4 190 inside the patch). The two sampling points outside the patch were located approximately 1 m
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6 191 upstream from its leading edge (U) and 1 m downstream from its rear edge (D). The four
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8 192 sampling points inside the patch were located at 10%, 30%, 50%, and 90% of the canopy length,
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10 193 starting from the leading edge. For each position, the velocity profile was measured, and a core of
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12 194 sediment was collected (5 cm diameter and 10 cm deep).
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17 18 19 196 *Hydrodynamic measurements and velocity profiles*

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21 197 Vertical profiles of velocity were measured using a 3D Acoustic Doppler Velocimeter
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23 198 (ADV, FlowTracker Handheld-ADV, SonTek, USA). Vertical profiles were made with depth
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25 199 intervals of less than 12 cm, reduced to 1 to 4 cm near plant-water interfaces. Due to the
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27 200 dimensions of the side-looking probe, measurements closest to the sediment were taken at a
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29 201 minimum of 4 cm above the channel bed. Velocity was recorded over 100 s at 1 Hz. Data were
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31 202 filtered to remove spikes (Goring and Nikora 2002; Mori et al. 2007). The time average (denoted
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33 203 by an over bar) of the streamwise (i.e. in the flow direction) velocity component, \bar{u} , was used to
34
35 204 quantify the flow modification induced by plant patches. From each time-averaged velocity
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37 205 profile, the velocity at 20 cm above the bed, \bar{u}_{20} , was estimated by interpolation. This distance
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39 206 was chosen to avoid bottom interference due to the presence of boulders and cobbles. Moreover,
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41 207 this choice allowed us to measure hydrodynamic forces faced by plants during their growth and
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43 208 the patch development in relation to the patch architecture. Please note that due to the plant
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45 209 morphology and patch architecture (i.e., flexibility of stems, patch height that increases along the
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47 210 patch, and L/h ratio), measurements at 20 cm of depth were located above the canopy for the
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49 211 smallest patches and at the upstream end of long patches. In these cases, \bar{u}_{20} may qualitatively
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51 212 capture changes in the velocity field due to lateral deflection of flow away from the patch, but
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53 213 they will definitely over-estimate the velocity within the canopy. Turbulence intensity was not
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214 included in our study: for the smaller patches, velocity measurements within the patch were
215 absent and this impeded the detection of turbulence variation within the patch from the leading
216 edge for different patch lengths.

217 To examine the effect of a plant patch on flow conditions within the patch, the 95%
218 confidence interval of the \bar{u}_{20} within the patch was calculated and compared to the \bar{u}_{20} value
219 measured at the upstream position ($\bar{u}_{20 U}$). Then, we calculated the fractional difference between
220 the local velocity, \bar{u}_{20} , and the velocity upstream of the patch, $\bar{u}_{20 U}$. That is, for each position
221 (10%, 30%, 50%, 90% and D), we defined $\Delta\bar{u}_{20} = (\bar{u}_{20} - \bar{u}_{20 U}) \times (\bar{u}_{20 U})^{-1}$. To assess whether the
222 effect of patch length on hydrodynamics differs between the two sites, we performed an analysis
223 of covariance (ANCOVA) using \bar{u}_{20} and $\Delta\bar{u}_{20}$ at the 50% position as the dependent variable, site
224 as the effect and patch length as a covariate. The interaction term was included in the model and
225 dropped if not significant. For the analysis of the relation of $\Delta\bar{u}_{20}$ and L, an outlier point was
226 omitted due to a very low $\bar{u}_{20 U}$ resulting from the interaction with an upstream patch.

227
228 *Sediment characterization*

229 After sampling, the collected sediment cores were stored at 4°C. To perform the effective
230 grain size analyses (i.e. for the whole sediment, without removal of organic matter, McCave and
231 Syvitski 1991; Phillips and Walling 1999), sediments were wet sieved with distilled water at 1.6
232 mm, separating the fine and the coarse fraction, and then dried at 70°C for 48 hours to allow
233 sample preservation until the analyses were completed. Grain size analyses of sediment were
234 performed in the aqueous phase by laser diffractometry using a Malvern Mastersizer 2000 G
235 (diameter range: 0.01 - 2000 μm). The analytical model used is based on the Fraunhofer theory,
236 which assumes spherical particles. Prior to the measurements, sediments were sonicated for 2 min

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4 237 to destroy the aggregated particles formed during the 70°C drying process (Badin et al. 2009).
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6 238 The results of the analysis are displayed as grain size distribution curves. The mode of the curve
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8 239 indicates the most abundant grain size in terms of the percentage per total solid volume. The
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10 240 curves were transformed into cumulative curves, and the percentile values $d_{0.1}$, $d_{0.3}$, $d_{0.5}$, were
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12 241 calculated (maximum diameter corresponding to 10%, 30%, and 50%, respectively, of the total
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14 242 particle volume). The three values were found to be correlated, and only the percentile value $d_{0.3}$
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16 243 was kept for further analyses. Measurements of grain size were conducted in triplicate for each
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18 244 sample, and mean values and standard deviations of $d_{0.3}$ were calculated. To describe the
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20 245 sediment texture at each sampling position, we used only the mean value of $d_{0.3}$, as the standard
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22 246 deviation was less than 10%.
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29 247 To assess the effect of the patch size on the sediment texture within the patch, the 95%
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31 248 confidence interval of the $d_{0.3}$ within the patch was calculated and compared to the $d_{0.3}$ value
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33 249 measured at the upstream position ($d_{0.3 U}$). Then, for each position (10%, 30%, 50%, 90% and D),
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35 250 we expressed the $d_{0.3}$ relatively to the $d_{0.3 U}$ to obtain the relative value $\Delta d_{0.3}$, as $\Delta d_{0.3} = (d_{0.3} - d_{0.3 U}) \times (d_{0.3 U})^{-1}$. The $\Delta d_{0.3}$ at the 50% position was used to assess whether the effect of patch length
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37 251 on sediment texture differs between the two sites. As the relationship between $\Delta d_{0.3}$ at the 50%
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39 252 position and patch length was not linear, we fitted for each site an exponential model following
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41 253 the equation $\Delta d_{0.3} = a + b e^{cL}$.
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50 256 **Results**

51 257 *Flow velocity*

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53 258 The streamwise velocity profiles upstream of the patches generally followed a typical
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55 259 boundary layer profile. At positions within the patches, \bar{u} was highest above the canopy,
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260 decreased just above the canopy, and usually reaching approximately zero within the canopy
261 (Online Resource 2).

262 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}
263 measured at the upstream position ($\bar{u}_{20 U}$) was very close or within the 95% confidence interval of
264 the \bar{u}_{20} values within the patch (Fig. 2a). For these short patches, the \bar{u}_{20} was stable along the
265 patch (Fig. 2a), because the measurement of \bar{u}_{20} was conducted above the canopy. For all the
266 longer patches but 2, the $\bar{u}_{20 U}$ was higher than the 95% confidence interval of the \bar{u}_{20} values
267 within the patch and the \bar{u}_{20} values gradually decreased along patches, with velocity close to zero
268 observed at the 90% position in longest patches (Fig. 2a).

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

279
280 *Sediment characteristics*

281 For short patches ($L \leq 0.3$ m), the $d_{0.3}$ measured at the upstream position ($d_{0.3 U}$) was
282 within or lower than the 95% confidence interval of the $d_{0.3}$ values within the patch, indicating

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

287 The relationship between $\Delta d_{0.3}$ at the 50% position and patch length was different at the 2
288 sites. For the HV site, the $\Delta d_{0.3}$ exponentially decreased with patch length ($\Delta d_{0.3} = 4.71e^{-4.39L} -$
289 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
290 reached a threshold value around -80% of $d_{0.3 U}$ (Fig. 4), corresponding to $d_{0.3} = 25 \mu\text{m}$ (data not
291 shown). For the LV site, even though the relationship between $\Delta d_{0.3}$ and patch length was not
292 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
293 between -13% and -67% of the $d_{0.3 U}$ for all the patches with $L > 0.3$ m, with a mean value of -
294 38%, corresponding to $d_{0.3} = 52 \mu\text{m}$ (data not shown).

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

297 The relationship among relative velocity ($\Delta \bar{u}_{20}$), grain size distribution ($\Delta d_{0.3}$) and patch
298 length can be summarized in a contour plot from the data relative to the 50% position, where the
299 effect of the patch on flow velocity and sediment characteristics is expected to be maximal (Fig.
300 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
301 plot), while for larger patches ($L > 1.1$ m), the increase in patch length generally results in
302 reduction in both $\Delta \bar{u}_{20}$ and $\Delta d_{0.3}$ (quadrant III of the plot).

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304 **Discussion**

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4 305 Patch structural characteristics are important factors that determine the capacity of a
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6 306 species to influence flow and sedimentation processes. The present study investigated the effects
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9 307 of patch size on these processes in order to test whether the effect of submerged plant patches on
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11 308 flow and sediment texture is dependent on patch size and whether this effect differs according to
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14 309 environmental conditions. Our results indicated that a minimal patch size is required to induce
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16 310 modifications of flow and sediment characteristics ($L > 0.3$ m and $L > 0.9$ m for the HV and LV
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18 311 sites, respectively for the flow, and $L > 0.3$ m for the sediment characteristics). Moreover,
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21 312 streamwise velocity decreased linearly with patch length independently of the site conditions
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23 313 (Fig. 3). However, the sediment texture was dependent on site conditions (Fig. 4): for the HV
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26 314 site, the $\Delta d_{0.3}$ in the middle of the patch exponentially decreased with patch length, reaching a
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28 315 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
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30 316 > 0.3 m.

317 318 319 *Effect of patch length on flow reduction*

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

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329 recirculation generated in the wake of the patch, *e.g.*, details of which are illustrated in figure 2 of
330 Folkard (2005).

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

340 The absence of an adjustment length (*i.e.*, an exponential reduction of the streamwise
341 velocity up to a distance from the leading edge over which no further modification of flow is
342 observable) in our data may indicate that the adjustment length was longer than the patch length
343 in all cases due to the patch architecture of *C. platycarpa*, characterized by a very dense, flexible
344 overhanging canopy and a positive correlation between patch height and length, which may lead
345 to a different flow pattern than patches with different architecture (Chen et al. 2013). In addition,
346 the positive relationship between patch height and length implies that the submergence ratio
347 (H/h) varies with patch length: very small patches ($L \leq 0.3$) are deeply submerged ($H/h > 10$; Table
348 1), whereas, for increasing length, patches become shallow submerged or even emergent, *i.e.* the
349 canopy reaches the water surface (H/h gradually decreases for increasing length, until values
350 close to 1, Table 1). The longest patches of *C. platycarpa* present a gradual decrease of the ratio
351 H/h from upstream to downstream, due to the flexibility and buoyancy of the canopy. As the H/h
352 ratio controls the relative importance of the turbulent stress at the top of the canopy and the

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353 pressure gradient of the flow (Nepf 2012), the variation of H/h with patch length may
354 consequently have an important role in flow and sedimentation patterns for different patch length
355 that deserves further investigations.

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

362 The capacity to modify the surrounding physical environment is a species-specific
363 property that depends on plant traits (Bouma et al. 2010; Sand-Jensen and Pedersen 1999). Plant
364 morphology and canopy architecture are important factors that determine the capacity of a
365 species to modify flow characteristics (Fonseca and Fisher 1986; Sand-Jensen 1998; Schoelynck
366 et al. 2014). A comparison of stiff and flexible species in salt marshes demonstrated how the stiff
367 species was the most efficient ecosystem engineer, where ecosystem engineer efficiency is
368 defined as the benefit–cost ratio per unit of biomass investment. Specifically, stiff species are
369 able to attenuate the wave energy with a slightly lower drag force per unit biomass (Bouma et al.
370 2010). Future studies may focus on lotic species with contrasting canopy architecture and patch
371 structure in order to test whether they present different patterns of flow reduction with increasing
372 patch length.

374 *Effect of patch length on sediment texture*

375 As previously demonstrated, we observed the accumulation of fine sediment within plant
376 patches (Sand-Jensen 1998; Schoelynck et al. 2013). In accordance with our first hypothesis, we

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4 377 demonstrated that the grain size within patches depends on patch size: small patches showed
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6 378 similar or coarser sediment compared to upstream conditions, and a minimum patch length was
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9 379 necessary for fine sediment accumulation that reduced the average grain size. At both sites, very
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11 380 short patches ($L \leq 0.3$ m) presented erosion or no effect on the sedimentation processes, as
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14 381 already observed in salt marsh environments for circular patches (Bouma et al. 2007). The
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16 382 increased grain size observed for short patches may be related to increased turbulence at the
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19 383 leading edge, resulting in enhanced erosion of fine particles. This process has been observed both
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21 384 in the field for submerged vegetation in streams (Cotton et al. 2006) and in laboratory studies
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24 385 with plant mimics (Zong and Nepf 2010; 2011). Above a minimal size ($L > 0.3$ m), finer
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26 386 sediment accumulation was observed. The reduction of velocity and turbulence within a patch
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29 387 favours the sedimentation of smaller particles (Hendriks et al. 2009; Liu and Nepf 2016; Sand-
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31 388 Jensen 1998; Schulz et al. 2003). In addition, suspended and bed-transported particles may be
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33 389 retained inside plant patches by collision with stems and leaves (Hendriks et al. 2008; Pluntke
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36 390 and Kozerski 2003). We demonstrated that the sediment texture distribution decreased
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38 391 exponentially as a function of patch length for the HV site, indicating that maximum sediment
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41 392 trapping was reached at a short length (approx. 1 m). For the LV site, even though the
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43 393 exponential relationship was not significant, the data suggest that the maximum sediment
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46 394 trapping potential was reached at $L = 0.33$ m.

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48 395 In agreement with our first hypothesis, with increasing patch length, the accumulation of
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50 396 fine particles of sediment inside the patch increases up to a threshold length over which patches
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53 397 showed similar sediment texture distribution independently of patch length. This threshold length
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55 398 may correspond to the adjustment length, X_D (Chen et al. 2013), observed for artificial patches in
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58 399 flume experiments. X_D is the distance from the leading edge over which the velocity changes
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60 400 inside the patch, which is a function of patch stem density and height. Once the patch length

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4 401 exceeds X_D , the in-patch velocity does not decrease further with increasing length, and so the
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6 402 grain size does not change with further increases in patch length. In agreement with our second
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9 403 hypothesis, the two sites presented two different thresholds (1 and 0.33 m for HV and LV,
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11 404 respectively) and minimum $d_{0.3}$ values (25 and 52 μm for HV and LV, respectively). The
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14 405 difference in sediment texture ($d_{0.3}$ values) can be considered as a fingerprint of the suspended
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16 406 sediment available at the site: sites with lower values (HV) may have finer sediment in
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19 407 suspension and therefore require lower velocities to deposit all ranges of suspended particle sizes,
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21 408 including the finest ones. Very low flow velocities are found only in long patches, and, therefore,
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24 409 the finest sediments are present only in the long patches (for HV, $L > 1.0$ m). Reciprocally, sites
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26 410 with a higher $d_{0.3}$ value (LV) may have suspended particles of larger dimension; in this case, even
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29 411 the finest range of particles available may also tend to deposit at higher near-bed velocities and
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31 412 therefore even in smaller patches (for LV, $L > 0.33$ m). The differences observed between the two
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34 413 sites may also be due to differences in plant morphology (*e.g.*, stem density), leading to different
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36 414 adjustment lengths (Chen et al. 2013). In this case, a minimum velocity would be reached at
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38 415 different patch lengths, resulting in different sediment deposition patterns. The process of fine
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41 416 sediment accumulation within a patch may thus be influenced by both site conditions and plant
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43 417 and patch characteristics. Moreover, our finding may be influenced by the uniform condition of
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46 418 the sites in which the study was conducted: other sites with more variable conditions (*e.g.*
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48 419 channel structure, flow temporal variability) may present more complex flow and sedimentation
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50 420 patterns.
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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

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4 444 demonstrated that the engineering effect of *C. platycarpa* increases with increasing patch length,
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6 445 likely as a consequence of the increase in the quantity of plants that intercept flow. The reduced
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9 446 velocity and increased sedimentation occurring within plant patches may lower the risk of plants
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11 447 suffering mechanical damage through the reduction of hydrodynamic forces (Sand-Jensen and
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14 448 Pedersen 2008; Schoelynck et al. 2012) and may increase nutrient availability due to the
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16 449 accumulation of fine sediment and associated nutrients, such as phosphorus (Sand-Jensen 1998).
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19 450 The effects of plant patches on flow and sediment characteristics may thus induce positive
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21 451 feedback for plants, favouring their growth and patch expansion. Future research must thus focus
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24 452 on the effect of patch length on nutrient accumulation and associated biogeochemical processes.
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597 **Table captions**

598
599 **Table 1** Characteristics of *C. platycarpa* patches measured at sites HV and LV: length (*L*), width
600 (*W*), maximum height (*h*), *L/W* and *L/h* ratios of patches, the water depth (*H*) and the depth of
601 submergence ratio (*H/h*). Measures were taken with a tape measure; however, note that the patch
602 dimension measurements have an uncertainty of a few centimetres due to the continuous
603 movement of the canopy with the current

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Figure captions

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

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

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

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627 **Fig. 4** Effect of patch length on sediment characteristics associated with the species *C.*
628 *platycarpa* for the two sites. Δd_{30} at the 50% position exponentially decreased with patch length
629 ($R^2 = 0.96$, $p < 0.05$ for HV and $R^2 = 0.40$, $p = 0.75$ for LV), and the relationship was different
630 between the two sites

631
632 **Fig. 5** Contour plot of the effect of patch length on both velocity ($\Delta \bar{u}_{20}$) and sediment
633 texture ($\Delta d_{0.3}$) at both sites measured in the centre of the patches (50% position). The contour plot
634 describes how the ecosystem engineer capacity of aquatic plant patches increases with patch
635 length. Small patches induce little to no modification of the physical habitat, with possible
636 negative feedback (*e.g.*, increased grain size related to increased turbulence at the leading edge,
637 quadrant I). With increasing patch size, habitat modification (*i.e.*, reduction of velocity and
638 reduced sediment texture) became more important (quadrant III) and should induce positive
639 feedbacks for plants. Please note that 1) quadrant II is an artefact of the contour plot as,
640 physically, a reduction in water velocity will always lead to a reduction in sediment texture and
641 never to an increase in it (indeed, none of the patches measured was included in this quadrant); 2)
642 quadrant IV results from our methodological approach (streamwise velocity measured at 20 cm)
643 that, for small patches ($L < 1.1$ m), detects the velocity acceleration above the patch ($\Delta \bar{u}_{20} > 0$)
644 and not the velocity reduction inside the canopy, with the latter inducing the reduction of the
645 sediment texture ($\Delta d_{0.3} < 0$)

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649 **Supplementary material captions**

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651 **Online Resource 1**

652 Sediment grain size distribution upstream of the patches of *C. platycarpa* at sites a) HV
653 and b) LV. Patch number corresponds to a patch of increasing length (see Table 1). Sediment
654 classification follows the Wentworth size classes (Wentworth 1922).

655

656 **Online Resource 2**

657 Time-averaged vertical profiles of streamwise velocity (\bar{u}) for patches of *C. platycarpa* of
658 increasing size (see Table 1). Velocity profiles were sampled in six positions along the main axis
659 of the patch: upstream (U, ▷), inside the patch at 10% (○), 30% (Δ), 50% (◇), and 90% (□) of its
660 length, and downstream (D, ▽). The dashed line indicates patch canopy height.

661

662 **Online Resource 3**

663 Cumulative curves of the grain size distributions of sediment in different positions along
664 the main axis of patches of *C. platycarpa*: upstream (U), inside the patch at 10%, 30%, 50%, and
665 90% of its length, and downstream (D).

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Figure 1 (black and white)

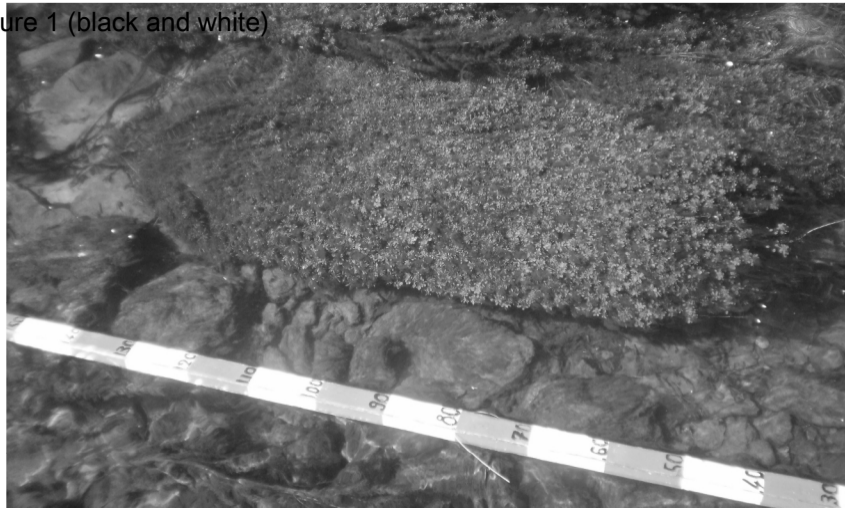
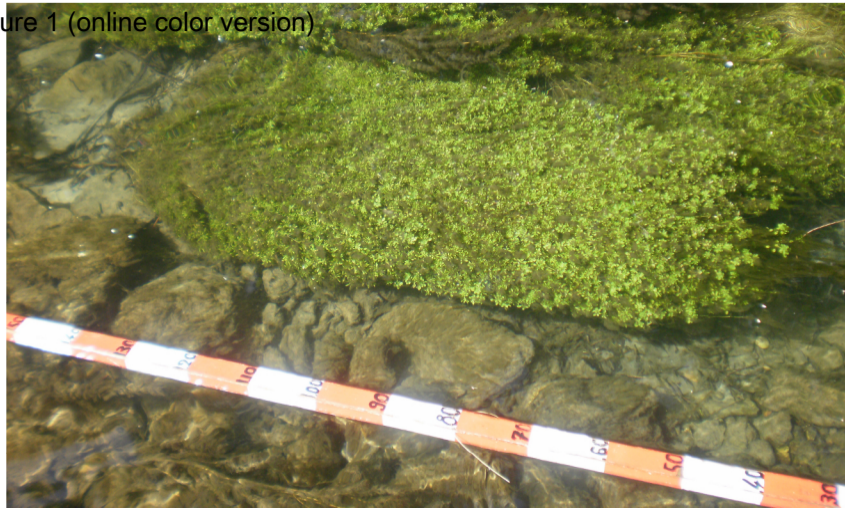


Figure 1 (online color version)



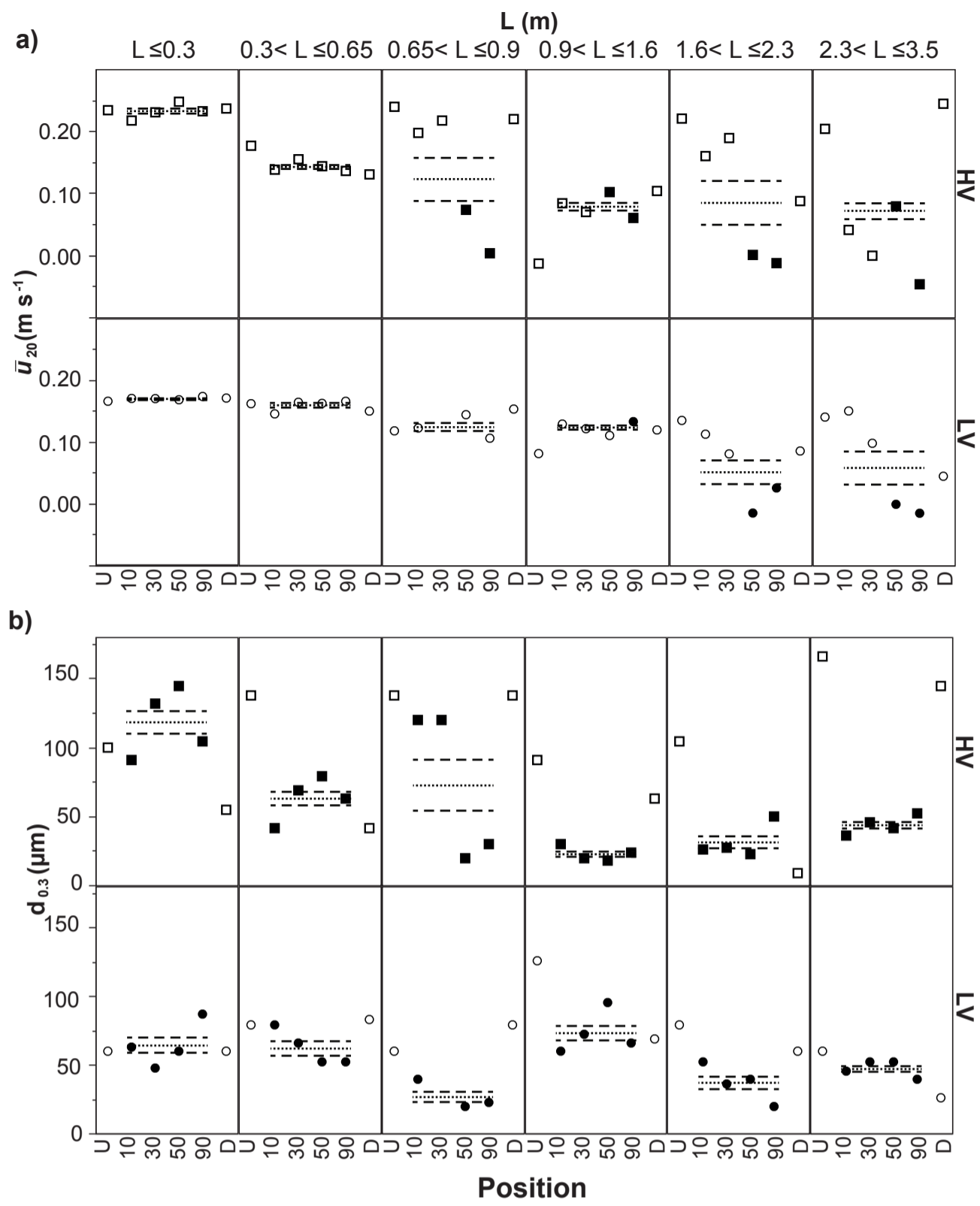


Figure 3

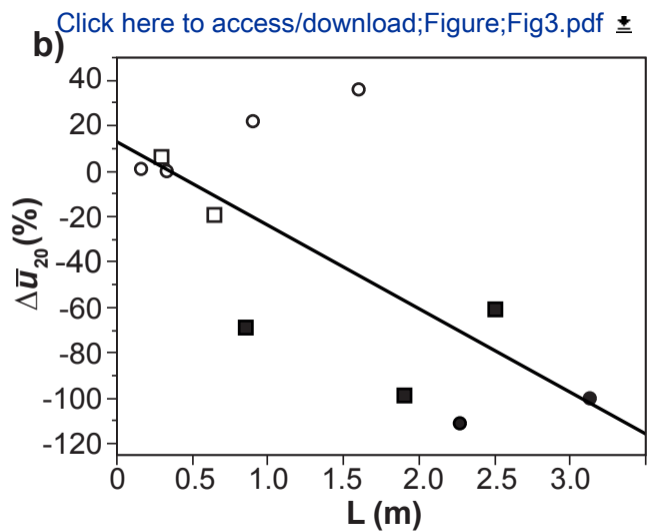
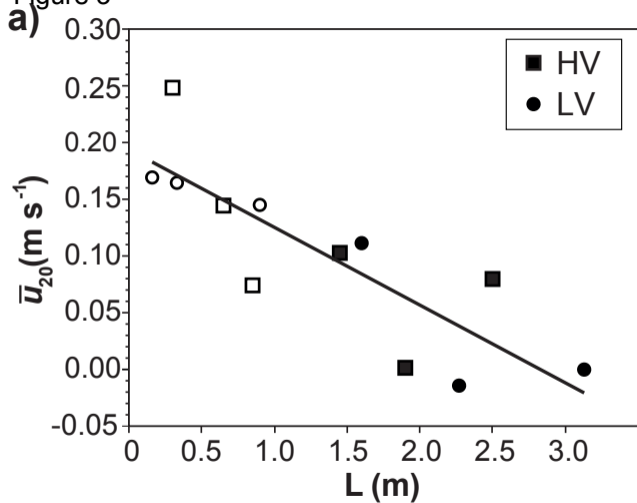
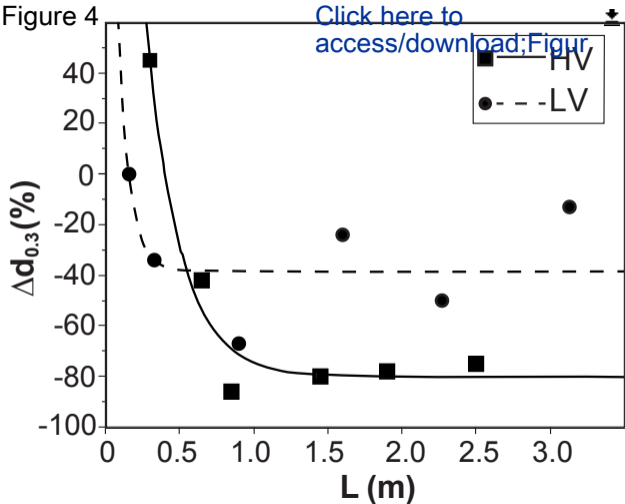
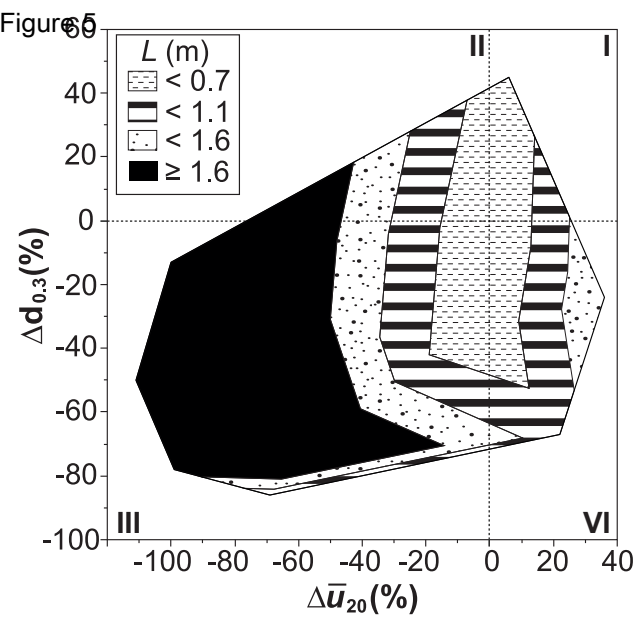
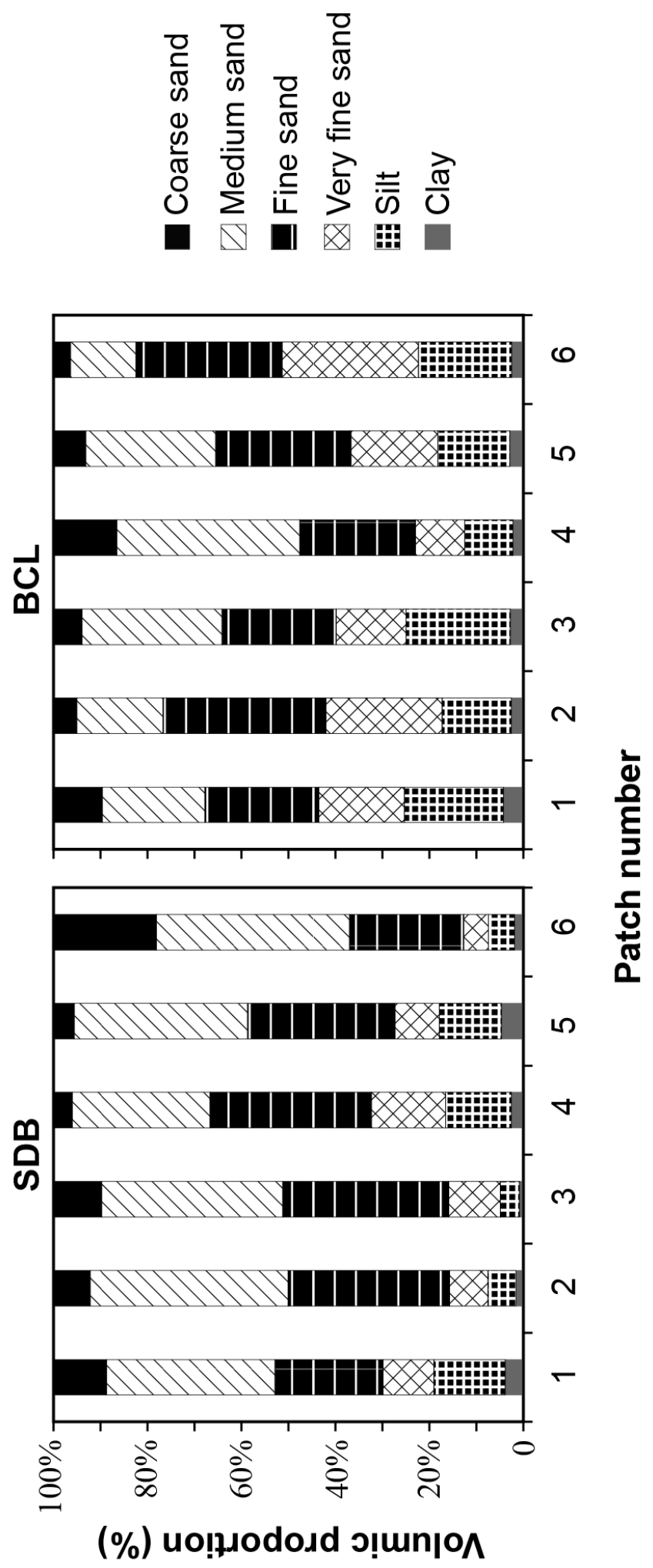
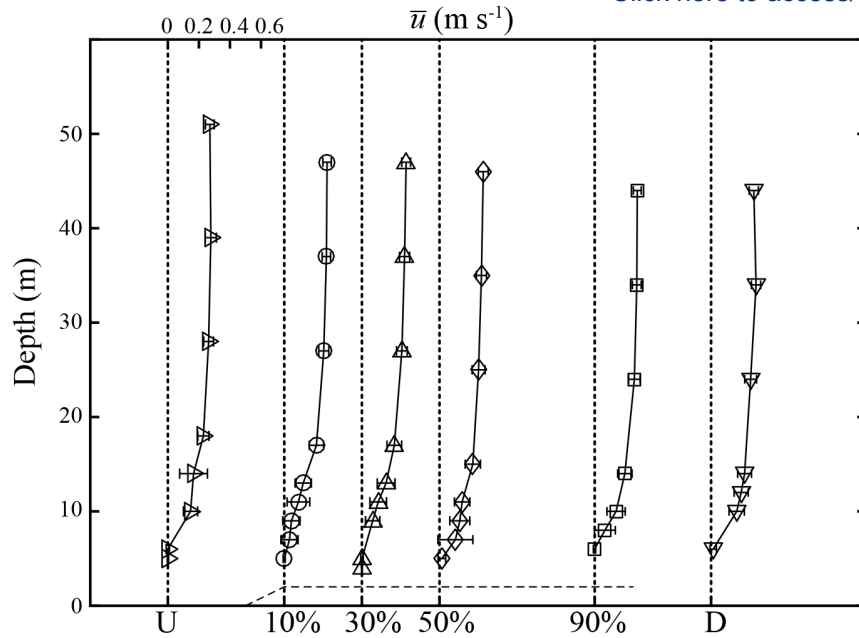


Figure 4

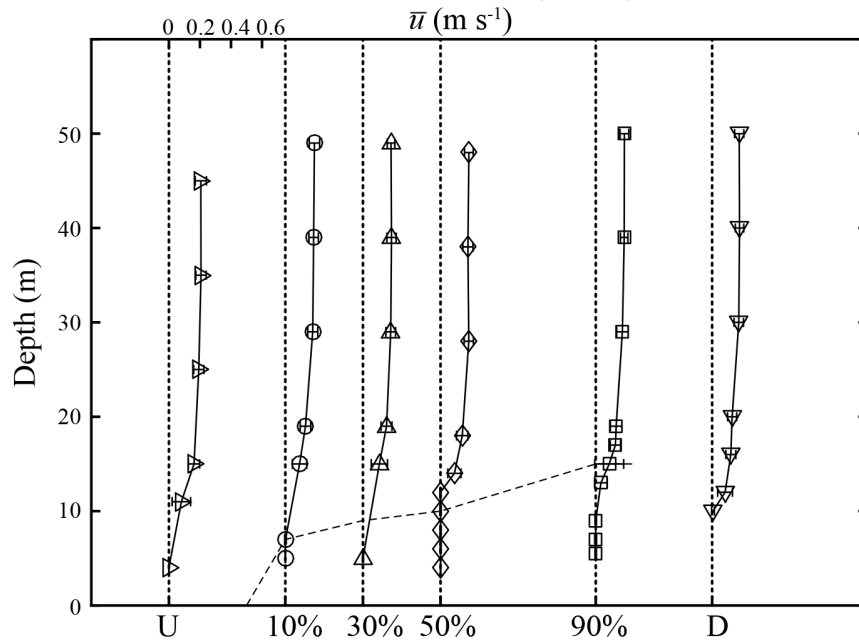




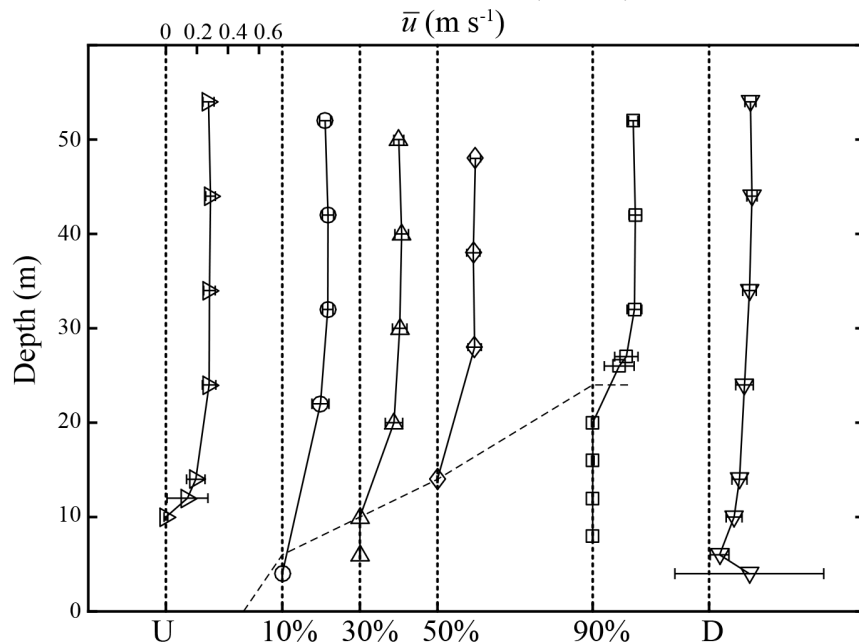




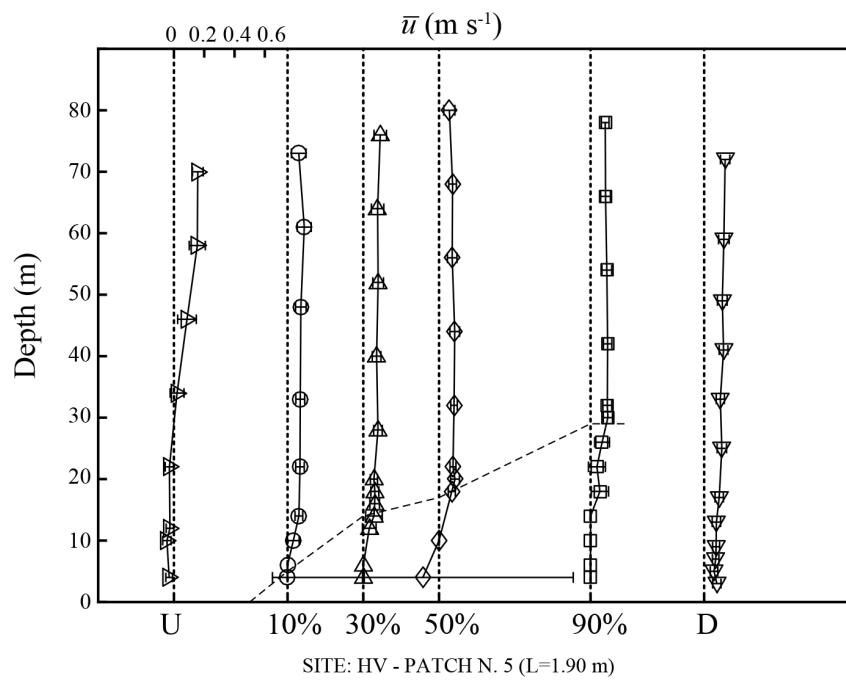
SITE: HV - PATCH N. 2 (L=0.65 m)



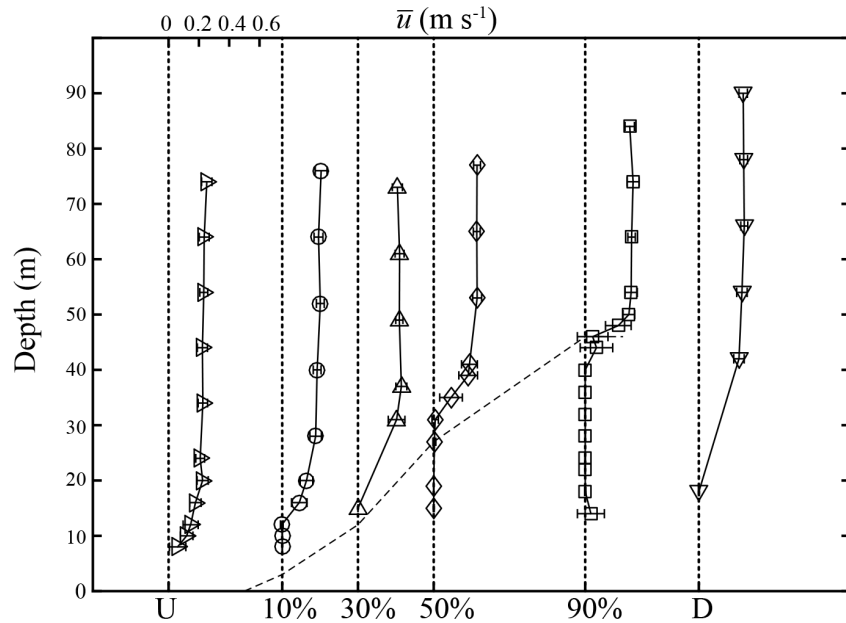
SITE: HV - PATCH N. 3 (L=0.85 m)



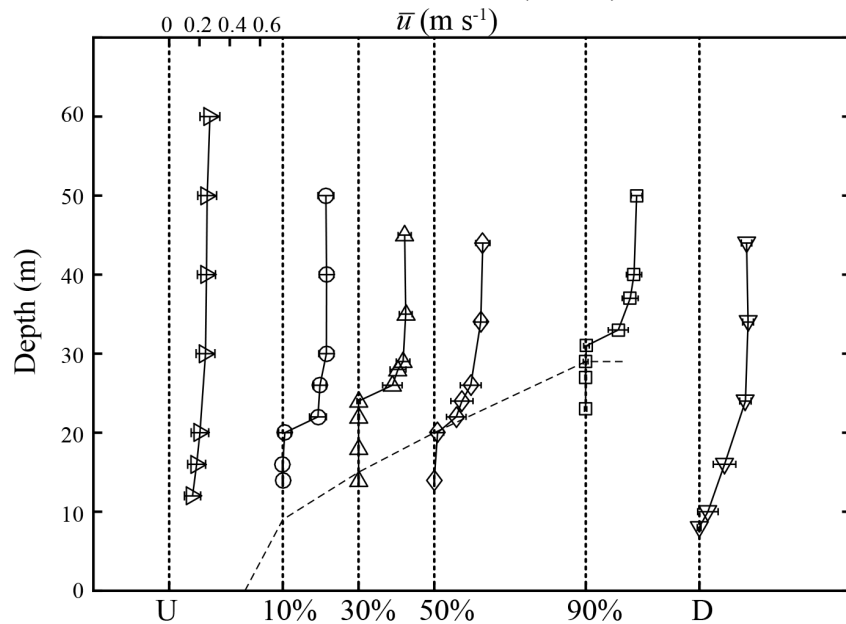
Position



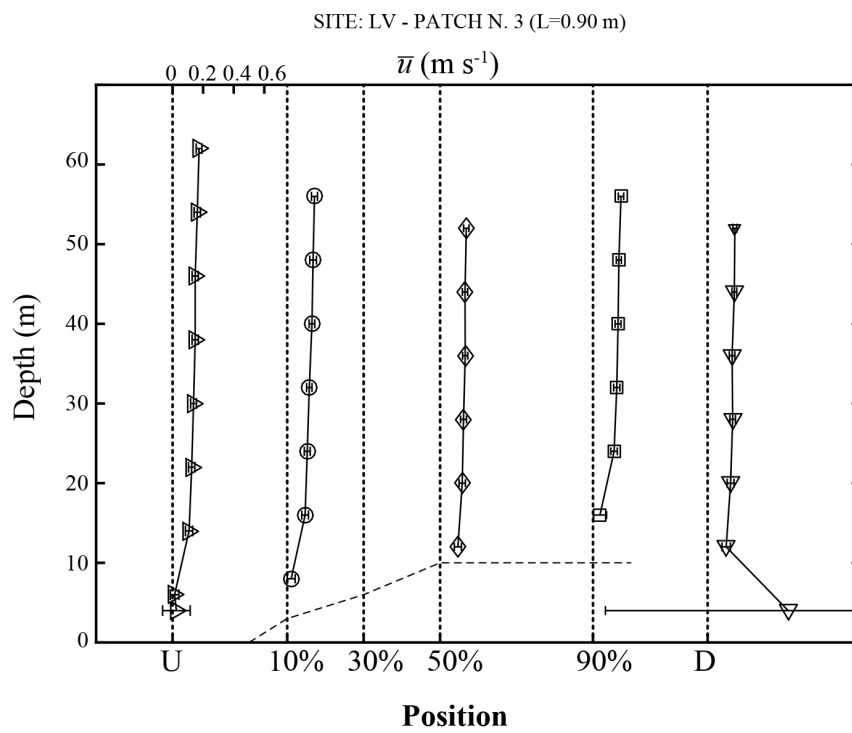
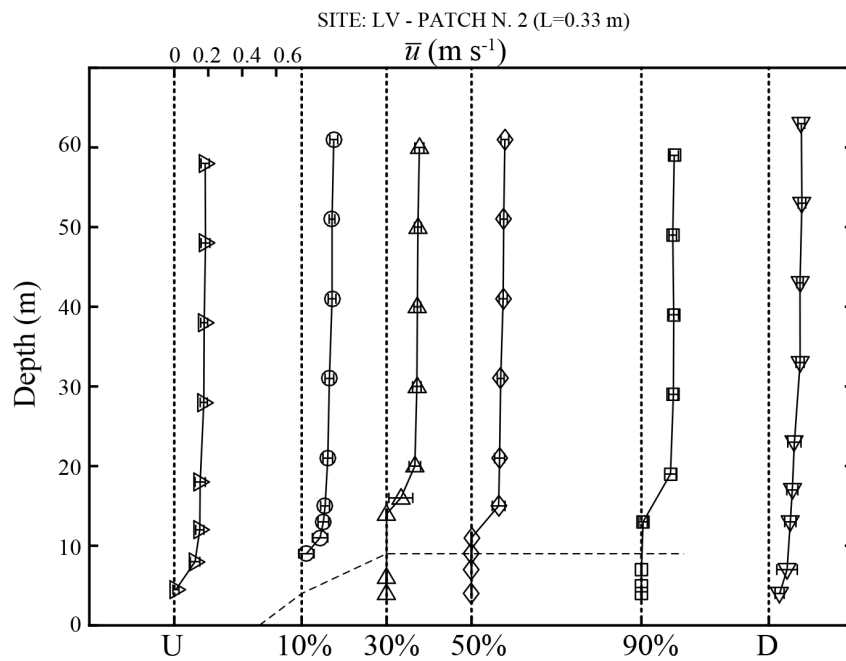
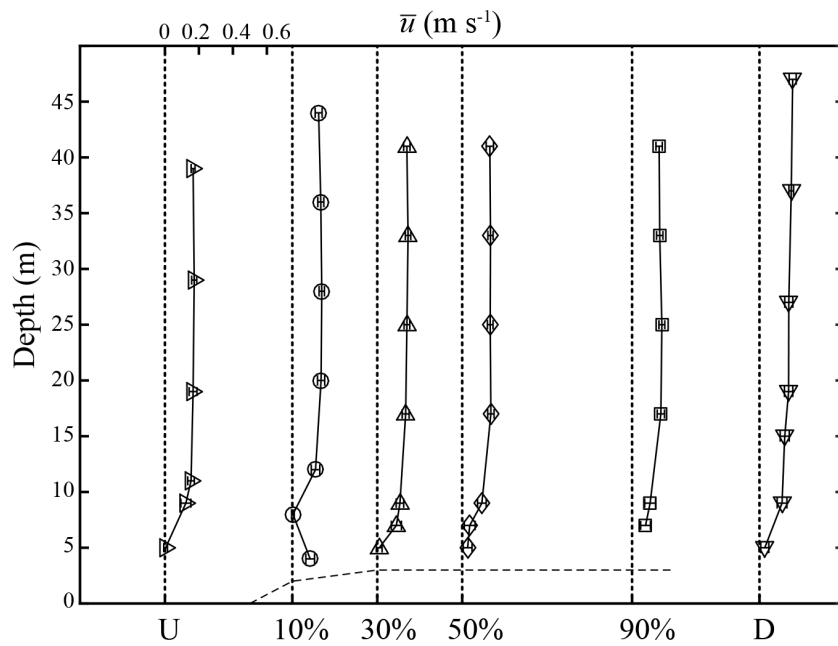
SITE: HV - PATCH N. 5 (L=1.90 m)

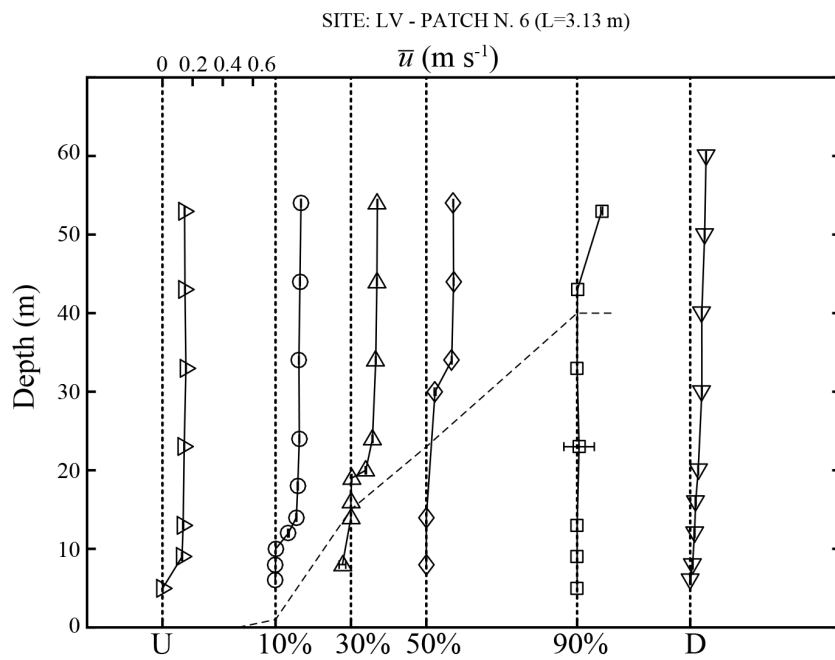
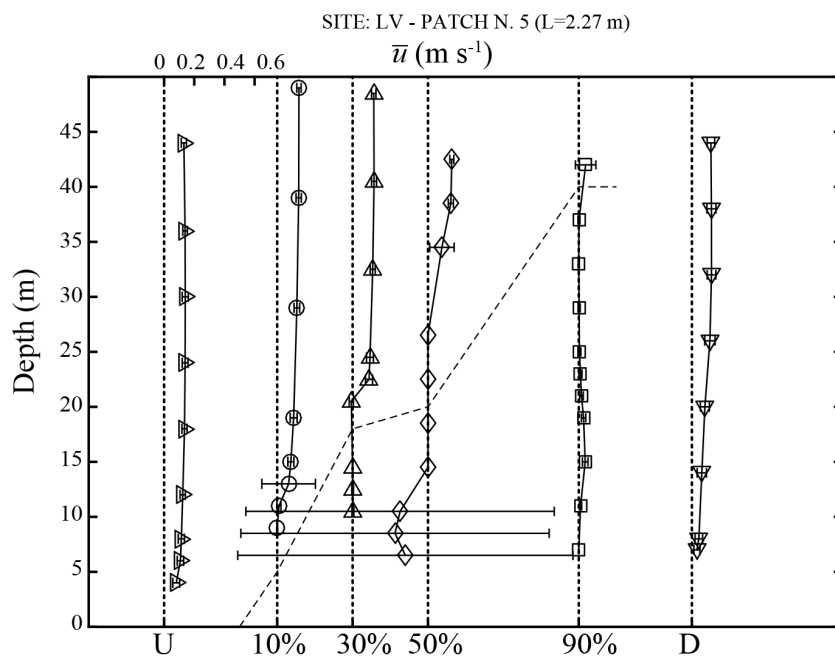
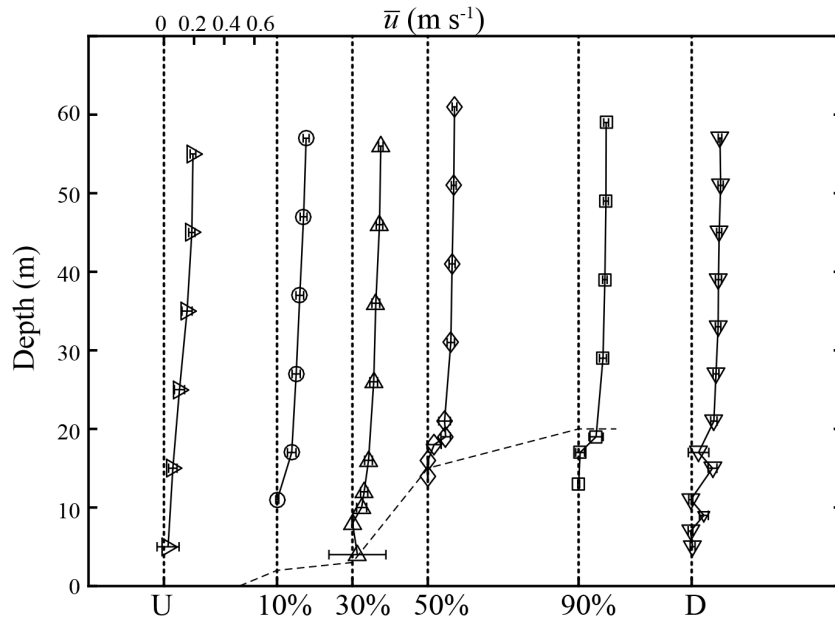


SITE: HV - PATCH N. 6 (L=2.50 m)

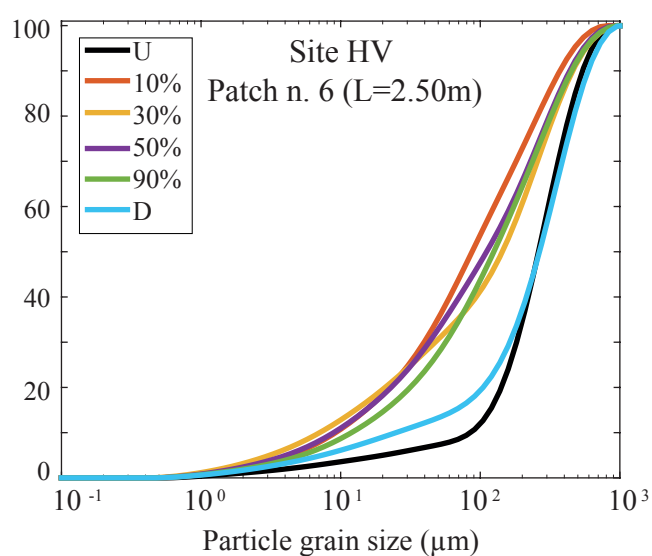
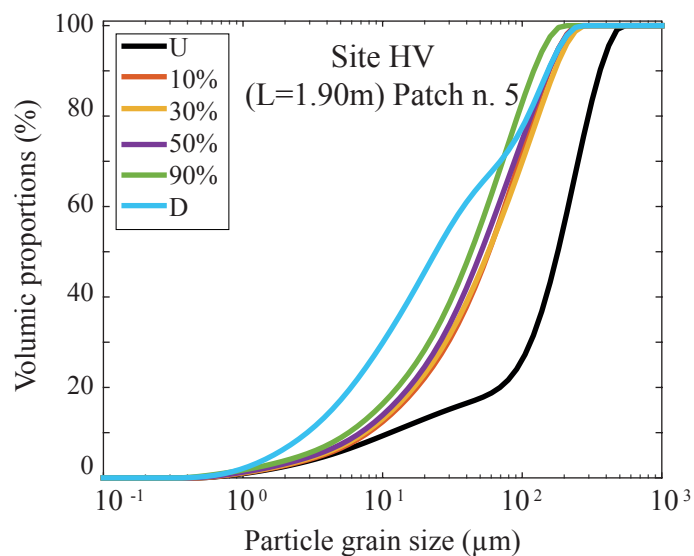
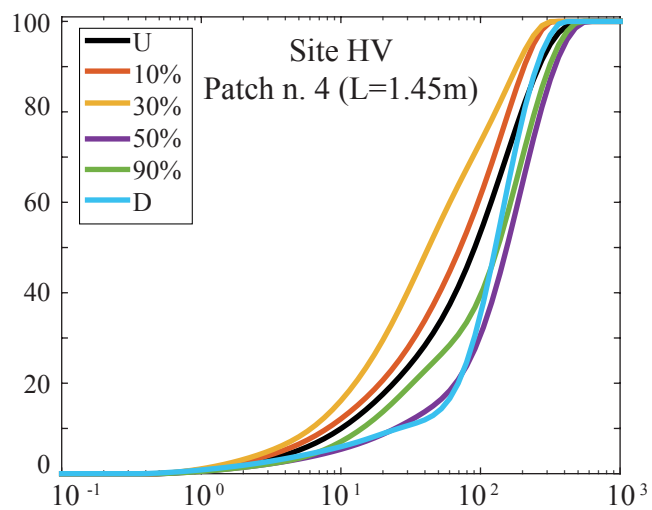
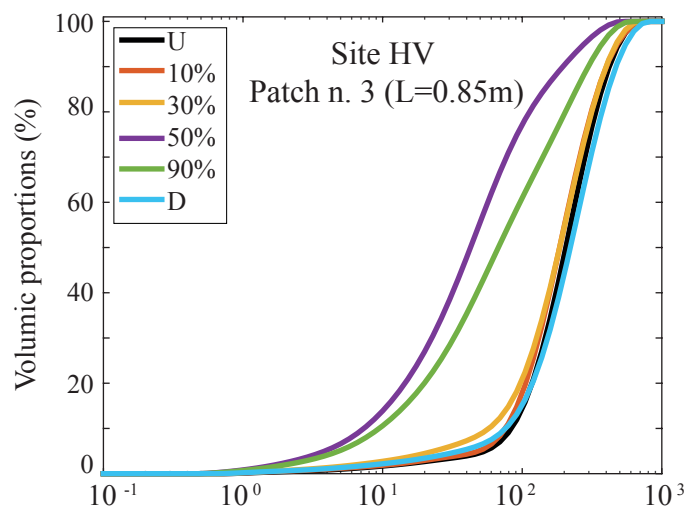
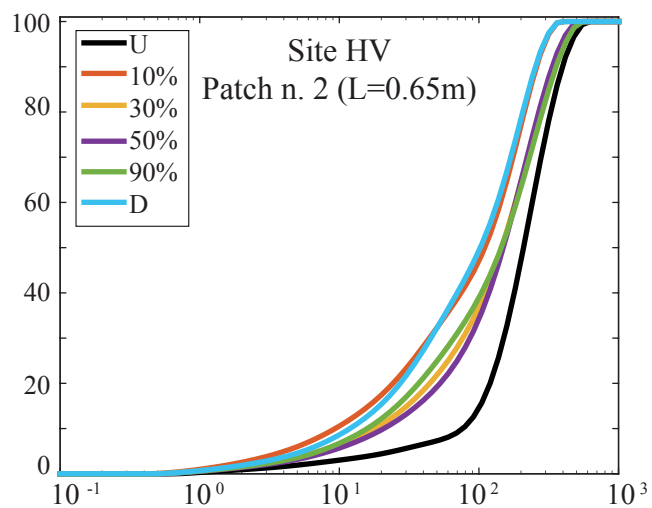
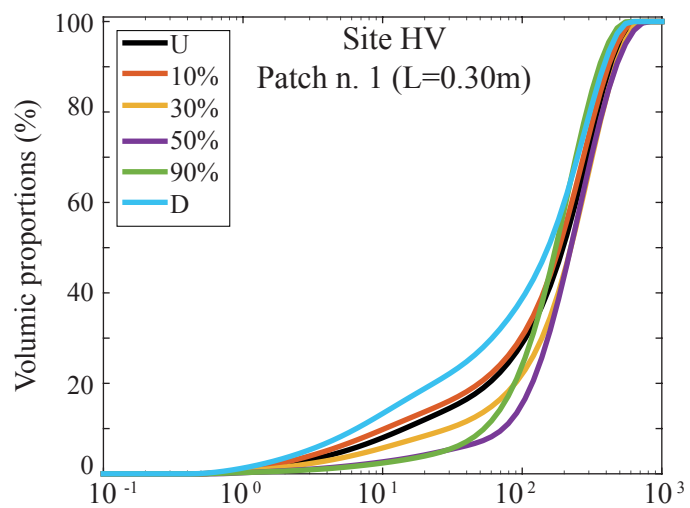


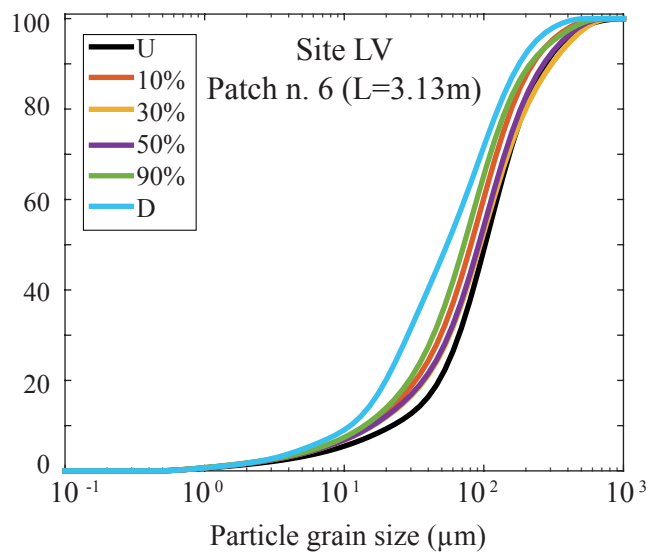
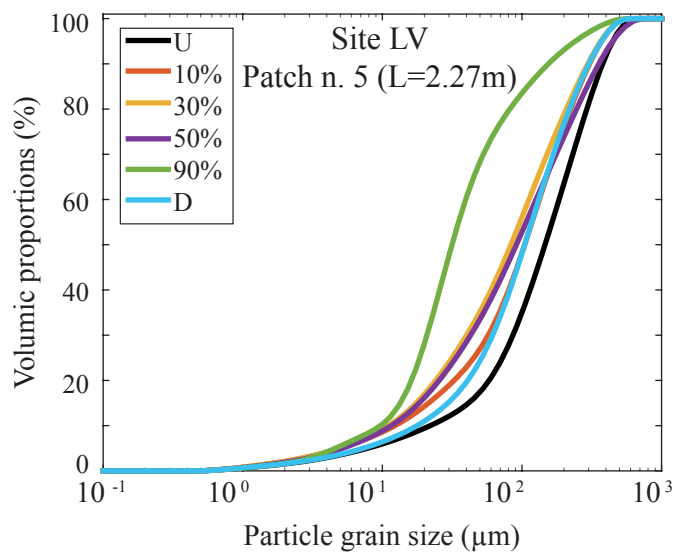
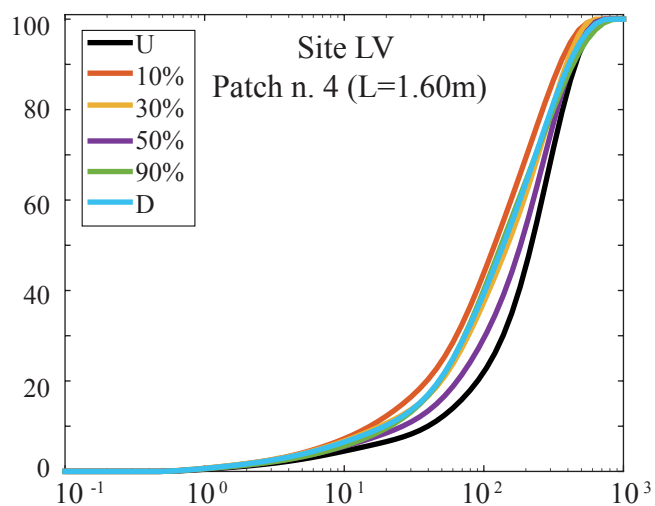
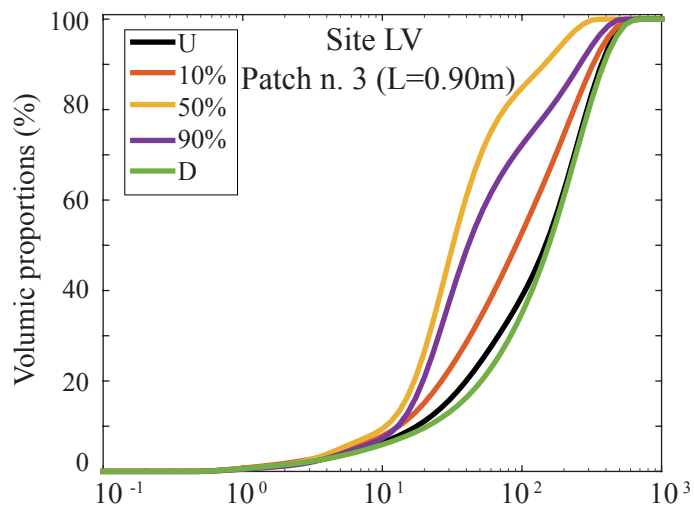
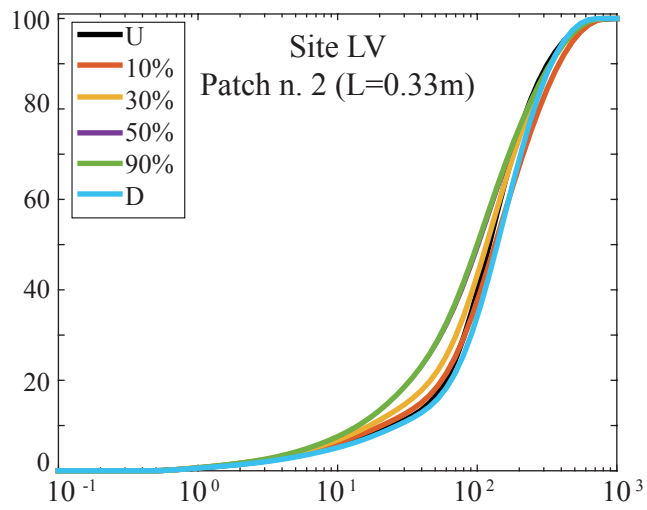
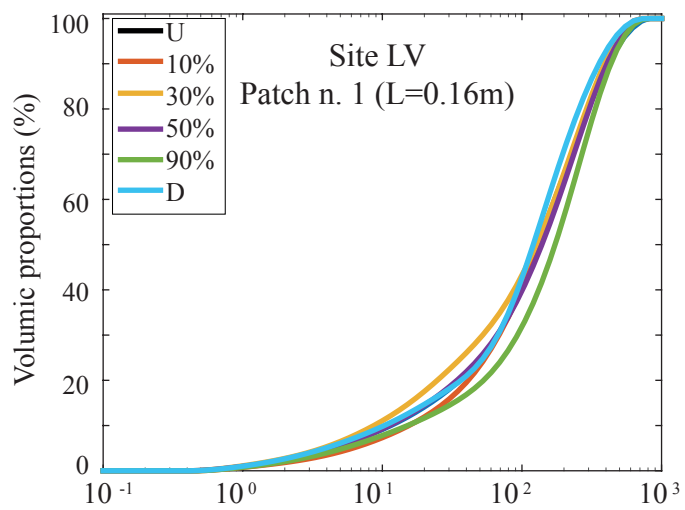
Position





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Site	HV						LV					
Patch N.	1	2	3	4	5	6	1	2	3	4	5	6
<i>L</i> (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
<i>W</i> (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
<i>h</i> (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
<i>L/W</i>	3	3.4	1.5	1.4	2.3	3.8	2	2.1	1.8	4	2.8	4.5
<i>L/h</i>	15	4.3	3.5	5	4.1	8.6	5.3	3.6	9	8	5.7	5.2
<i>H</i> (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
<i>H/h</i>	27	3.8	2.3	3.1	1.9	1.9	16	7.7	6.8	3.2	1.3	1.0