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1 **Flow and wake length downstream of live submerged vegetation patches:**  
2 **how do different species and patch configurations create sheltering in**  
3 **stressful habitats?**

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11

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15

16 **Key Points:**

- 17
- 18 • Vegetation patches in stressful habitats shelter organisms from hydrodynamic forces.
  - 19 • The sheltering effect is influenced by two fundamental patch dimensions (i.e., canopy  
20 half-width and height) and by patch density.
  - 21 • Flow attenuation behind channel-spanning patches prevails for longer distances than  
22 for finite-width patches.

22

23 **Abstract**

24 Vegetated canopies modify water conveyance and bed stabilization in aquatic ecosystems,  
25 providing shelter for other organisms. The sheltering effect downstream of a canopy is  
26 however rarely quantified for live vegetation, and it is unknown how this effect is influenced  
27 by vegetation patch configuration and characteristics. We measured the sheltering effect of  
28 different species and patch configurations by comparing the length of the steady wake region,  
29 defined in this study as (1) the zone where streamwise velocity is diminished to more than  
30 half of the incoming velocity ( $L_{w1}$ ), and (2) the distance downstream of the patch where  
31 velocity begins to increase ( $L_{w2}$ ). Then, we measured the drag experienced by a plant at  
32 different downstream locations as a measure of sheltering for plants growing in the steady  
33 wake. We found that  $L_{w1}$  for channel-spanning cases was longer than for finite-width cases  
34 and extended to  $\geq 2.5$  patch lengths from the patch leading edge, while  $L_{w2}$  for finite-width  
35 patches was related to the smallest dimension between canopy half-width and height. Species  
36 effects were consistent across definitions: the species with the longest wake lengths was *G.*  
37 *densa*, followed by *C. platycarpa* and *V. spiralis*, which showed similar wake lengths for  
38 finite-width cases. Drag reduction was related to downstream flow modification for finite-  
39 width patches, but not for channel-spanning ones. The results of this study indicate that  
40 patterns of hydrodynamic sheltering behind live patches can be complex and difficult to  
41 predict based only on patch dimensions, especially due to co-variation between patch  
42 characteristics in real vegetation.

## 43 **1 Introduction**

44 Many ecosystems are modified by the actions or physical structure of organisms called  
45 ecosystem engineers (Jones et al., 1994). In aquatic environments, macrophytes act as  
46 important engineering species (Gurnell, 2014). They affect nutrient cycles and provide food  
47 and shelter for other organisms, such as fish and invertebrates (Haslam, 1978; Franklin et al.,  
48 2008). Vegetation promotes the deposition of finer, nutrient-rich sediment (Cotton et al.,  
49 2006; Wharton et al., 2006) and, at a larger scale, can affect geomorphic adjustments and  
50 landscape evolution (Gurnell & Grabowski, 2016). Vegetation also plays an important role by  
51 modifying hydrodynamic forces, water conveyance and bed stabilization (Sand-Jensen &  
52 Mebus, 1996; Sand-Jensen, 1998; Sukhodolov & Sukhodolova, 2009; Nepf, 2012).

53 In running water habitats, vegetation often grows in patches, which are relatively  
54 well-defined areas that differ from their surroundings (Forman, 1995). Patches generally  
55 consist of a single species at a relatively high density, and their spatial properties (e.g., length,  
56 width) are identified by sharp edges compared to surrounding bare areas (Schoelynck et al.,  
57 2018). Flow velocities are attenuated and sedimentation is enhanced within the patches  
58 (Bouma et al., 2007; Schoelynck et al., 2012; Licci et al., 2019); turbulence can either be  
59 reduced inside the patches and promote sediment deposition (Schulz et al., 2003; Hendriks et  
60 al., 2008), or it can increase at the plant stem scale, leading to resuspension of sediments  
61 (Tinoco & Coco, 2016). Flow velocity and turbulence are also reduced downstream of the  
62 canopy, leading to increased fine sediment deposition (Sand-Jensen, 1998). Although  
63 sediment deposition is enhanced behind the vegetation, scour patterns tend to form around the  
64 vegetation (Bouma et al., 2007; Chen et al., 2012a; Follett & Nepf, 2012; Yager &  
65 Schmeckle, 2013) and partly contribute to the deposition behind vegetation patches. This  
66 flow velocity reduction creates a sheltered region downstream of the vegetation, which is  
67 considered a major process for the functioning of running water ecosystems (Cornacchia et  
68 al., 2018; Baladrón et al., 2021). In physically harsh environments, a reduction in  
69 environmental stress is important for the structure of natural communities (Bertness &  
70 Callaway, 1994; Bruno et al., 2003). Running water habitats produce highly challenging  
71 conditions (Denny, 1988; Vogel, 1994), with a continuous risk of mechanical failure,  
72 dislodgement and downstream transport. Therefore, vegetation patches represent a major  
73 shelter for several types of organisms. For example, macrophyte patches generate a protected  
74 environment allowing the development of dense invertebrate communities (Gregg & Rose,  
75 1985). Flow reduction by vegetation may also facilitate larger organisms (e.g. fish; Baladrón  
76 et al., 2021), which, contrary to small-sized species, cannot escape from currents by  
77 occupying the boundary layer (of reduced velocity) on the sediment surface (Dodds & Hisaw,  
78 1924; Brooks et al., 2005; Carlson & Lauder, 2011). Vegetation can be considered a primary  
79 shelter of flowing environments due to its relatively large, three-dimensional structure, and  
80 for the creation of near-zero flow velocities in an otherwise running habitat (Sand-Jensen,  
81 1998).

82 The presence of vegetation can partially reduce the stressful conditions of running  
83 water habitats in two primary ways. First, sheltering by vegetation can reduce drag forces  
84 (Barsu et al., 2016), which limit the colonization of running habitats by large organisms that

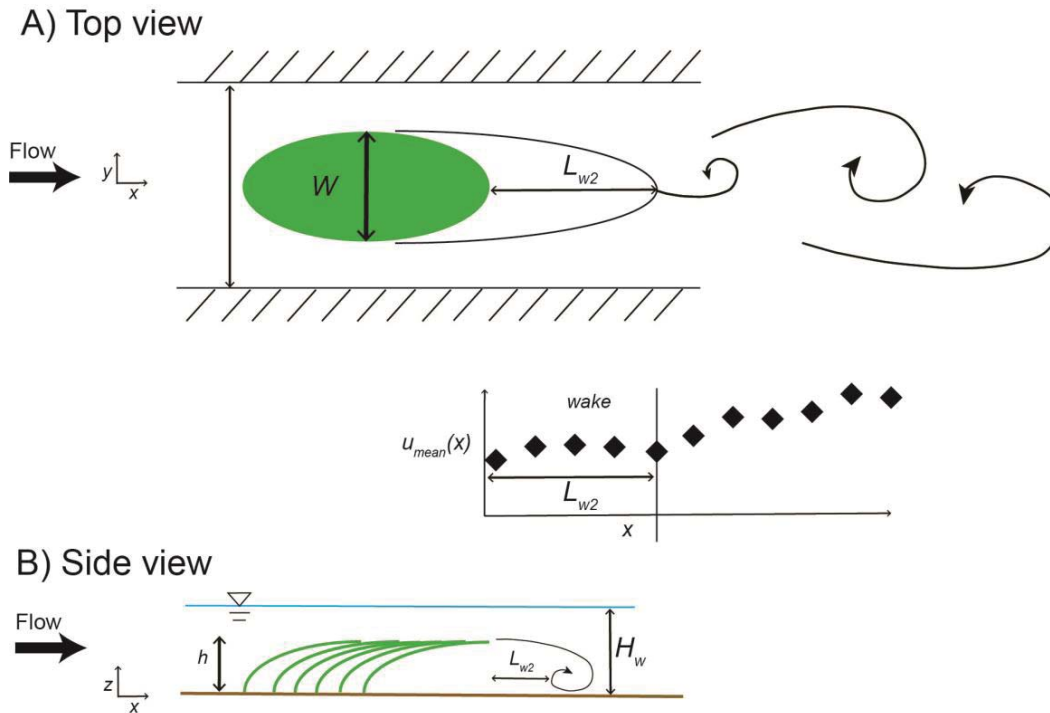
85 occupy the whole water column, such as plants (Biggs, 1996). Second, vegetation reduces  
86 bed shear stress, an index of force per unit area on the bed that influences macroinvertebrates  
87 living in this zone of velocity gradient (Statzner et al., 1988), and that has been related to  
88 sediment erosion and transport (Van Rijn, 1993). Therefore, vegetation promotes the  
89 deposition of nutrient-rich fine sediment (Sand-Jensen, 1998) and supports microbial activity  
90 (Caffrey & Kemp, 1992), while a high bed shear stress can lead to fine sediment erosion and  
91 poor nutrient availability. The influence of vegetation on these physical components of the  
92 habitat gives rise to a niche with low stress in a highly stressful environment, which can  
93 increase biodiversity (Cornacchia et al., 2018).

94 Despite the fundamental role of vegetation sheltering in ecosystem functioning, little  
95 is known about flow adjustments downstream of a vegetated canopy in the case of live  
96 macrophytes. In particular, the distance over which vegetation provides sheltering is rarely  
97 quantified, and little is known about its variability in response to different vegetation  
98 distributions and characteristics. The sheltered area might differ for channel-spanning  
99 vegetation that is uniform in the horizontal plane (Kouwen & Unny, 1973; Nepf & Vivoni,  
100 2000; Chen et al., 2013) compared to patches of finite width and length wherein there exists a  
101 gap between the patch and its neighbouring walls (Sand-Jensen & Vindbæk Madsen, 1992;  
102 Bouma et al., 2009; Zong & Nepf, 2012). In terms of vegetation characteristics under natural  
103 conditions, previous studies have shown that macrophyte species with contrasting  
104 morphologies create different velocity patterns downstream of their patches (Sand-Jensen &  
105 Mebus, 1996; Sand-Jensen, 1998). However, patch size, shape, or local variations in flow  
106 velocity and depth were not controlled in these field studies. This limits our ability to  
107 compare different species and generalize, or even predict their sheltering effect.

108 A more detailed, experimental description of the flow adjustments downstream of  
109 submerged vegetation patches comes from laboratory fluid mechanics studies, which often  
110 use plant mimics. The steady wake length ( $L_w$ ) is a region where velocity and turbulence are  
111 diminished compared to the free stream (Zong & Nepf, 2012) and is strongly influenced by  
112 turbulent structures promoted within the patch. In rigid canopies, stem-scale turbulence (Liu  
113 et al., 2018) is promoted by individual stems, with a horseshoe vortex forming at the toe and  
114 von Karman vortices of vertical axis (Stoesser et al., 2006). These stem scale eddies interact  
115 within the canopy and can disappear or merge in larger structures (Chang & Constantinescu,  
116 2015; Liu et al., 2021). Eddies may form at the patch scale: a larger horseshoe vortex around  
117 the toe of the patch (Liu et al., 2021), Kelvin-Helmoltz vortices at the canopy top (Raupach et  
118 al., 1996), and downstream von Karman vortices and a recirculation in the vertical  
119 streamwise plane (i.e., of horizontal crosswise axis; Marjoribanks et al., 2014; Liu et al.,  
120 2018). According to their size, interaction, and intensity, these eddies affect the velocities  
121 within the wake and its capacity for sheltering and sediment deposition. This was addressed  
122 in recent field experiments by Przyborowski and Łoboda (2021) and Biggs et al. (2019), who  
123 also emphasized the role of the biomass distribution along the vertical direction. This study  
124 investigates the influence of the plant species and density, and focuses on time-averaged  
125 characteristics, velocity and forces.

126 The sheltered area induced by the presence of vegetation can be determined from the  
127 steady wake length. Flume studies have shown that the location and structure of vortices  
128 behind a submerged patch determine the wake length (Hu et al., 2018; Liu et al., 2018) and  
129 are influenced by the ratio between patch width ( $W$ ) and height ( $h$ ) (Liu et al. 2018; Figure 1).  
130 Von Karman vortices cause lateral free-stream/wake momentum exchange, with a diffusion  
131 along  $W/2$  from the wake boundary to its central plane. The flow above the canopy promotes  
132 crosswise, horizontal vortices causing momentum exchange from top to bottom, with a  
133 diffusion along  $h$ , from canopy top to river bed. The so-called aspect ratio ( $W/h$ ) might  
134 markedly influence the wake length, by acting on the top to side velocities ratio, the vortices  
135 formation and the length required for momentum diffusion. Considering  $B$  as the channel  
136 width, the so-called patch confinement ( $W/B$ ) is also expected to be influential, by modifying  
137 the side velocity and also by suppressing the side velocities in aid of the top velocity alone in  
138 the spanning configuration ( $W/B = 1$ ). Particularly, the steady wake length increases with  
139 patch drag, which is generally described through the nondimensional flow blockage  $C_d a D$ ,  
140 where  $C_d$  is the drag coefficient for the plants within the patch,  $a$  is frontal area per unit  
141 volume, and  $D$  is patch diameter (Chen et al., 2012b). Flume studies with vegetation mimics  
142 have shown that the steady wake length can range from a few to approximately 20 cm ( $L_w/W$   
143 = 0.4–1.8 for a patch width  $W = 10$  cm) (Liu et al., 2018) and it is influenced by  
144 characteristics such as density (Chen et al., 2012b; Zong & Nepf, 2012; Chang &  
145 Constantinescu, 2015), flexibility (Hu et al., 2018) and patch geometry (Liu et al., 2018).  
146 These are relevant characteristics that vary widely for natural aquatic vegetation: plant  
147 patches occur in a range of sizes and aspect ratios ( $W/h$ ) (Sand-Jensen & Madsen, 1992;  
148 Schoelynck et al., 2012), morphological and mechanical properties (Puijalon et al., 2011) and  
149 vegetation density (Bouma et al., 2007; Peralta et al., 2008). For example, Przyborowski et al.  
150 (2019) investigated the flow downstream of two flexible aquatic plant species under natural  
151 conditions and revealed a weaker effect on the flow field compared to rigid mimics.  
152 However, the impact of vegetation characteristics on the steady wake length downstream of  
153 real vegetation remains largely untested. Differences in wake lengths induced by real plants,  
154 as opposed to artificial plants, can be expected for several reasons. For example, differences  
155 may be due to material properties at the single plant scale (properties of artificial materials vs.  
156 plant tissues such as stiffness or buoyancy but also heterogeneity of material arrangement  
157 observed in plants) that determine their reconfiguration and to the spatial arrangement of  
158 material that constitutes the patch (e.g., relatively irregular spatial patterns observed with live  
159 vegetation or highly branched structures of certain macrophyte species as opposed to the  
160 simplified structure of artificial patches). Finally, different patch characteristics co-vary in  
161 real vegetation, as patch length, width and height (Licci et al., 2019), but likely also other  
162 characteristics such as patch density, with small patches at the beginning of their growth  
163 having possibly sparser density, compared to larger ones.

164



165

166 **Figure 1.** Schematic representation of the flow patterns behind a submerged vegetation patch with  
 167 flexible stems. The development of vortical structures in the **a)** horizontal and **b)** vertical planes  
 168 controls the wake length  $L_{w/2}$  (distance downstream of the patch before the velocity along the patch  
 169 centreline begins to increase) and depends on patch density (Zong & Nepf, 2012), as well as patch  
 170 width ( $W$ ) and height, defined in this study as the deflected vegetation height ( $h$ ). Modified from Liu  
 171 et al. (2018).

172 In this study, we focus on how the steady wake downstream of live macrophyte patches  
 173 depends on the lateral confinement of vegetation (channel-spanning vs. finite-width patches)  
 174 and plant characteristics, and on their consequences for drag force reduction behind the  
 175 patches (an ecologically relevant process and an integral measure of plant adaptation to the  
 176 flow; Siniscalchi and Nikora (2012)). Specifically, we test the hypothesis that, for a patch of  
 177 given size and shape, different macrophyte species generate different steady wake lengths  
 178 based on their morphological characteristics and biomechanical traits. Within each  
 179 configuration, we vary (1) the patch aspect ratio ( $W/h$ ), (2) the macrophyte species, and (3)  
 180 the shoot density. Then, we assess the direct sheltering effect of these species by measuring  
 181 the drag force on a plant located at different distances downstream of the patch. Although the  
 182 growth of a plant would be different under natural conditions, the objective of this study is to  
 183 provide a realistic quantification of the drag forces experienced by plants that attempt to  
 184 establish and grow in the steady wake region.

## 185 2 Materials and Methods

### 186 2.1 Experimental channel

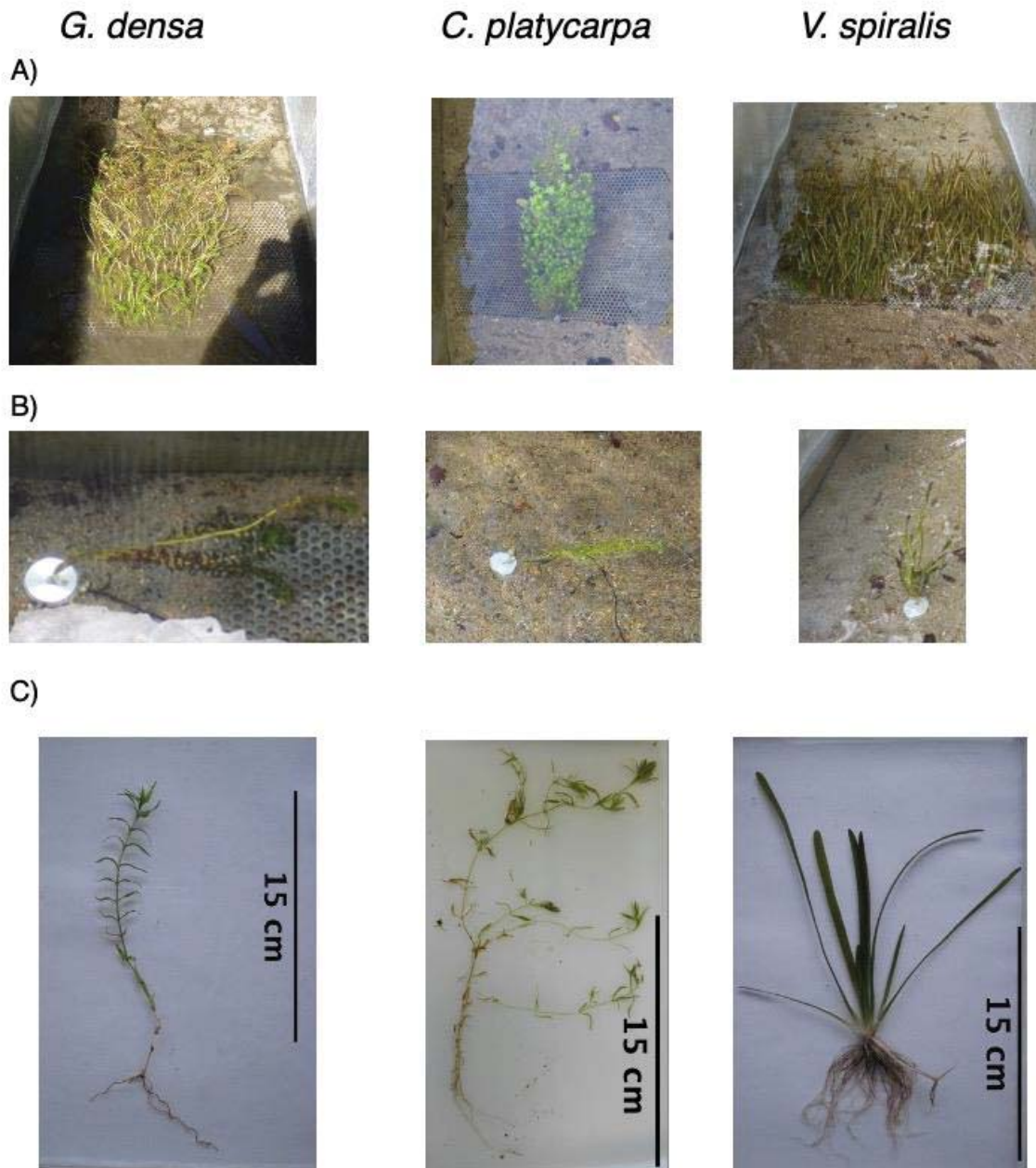
187 Experiments were performed in an outdoor flume located in the experimental garden on the  
 188 campus of University Lyon 1. The channel has a straight rectangular section; is 0.8 m wide  
 189 and 10 m long; and has a bed slope of 0.5%. The channel empties into a small, downstream  
 190 pond, through a downstream rectangular weir with an adjustable sharp crest. The water is  
 191 provided in the channel by two pipes from the combination of recirculated water from this  
 192 downstream pond and of water from an upstream groundwater supply. The water temperature  
 193 underwent limited daily variations during the experiments and thereby did not influence  
 194 viscosity; the water temperature in the open-air channel during all measurements ranged  
 195 between 15.9 and 20.7 °C and was on average 18.7 °C, as measured by the temperature  
 196 sensor embedded in the Vectrino II profiler (Section 2.5). The water exits via pipes into a  
 197 stilling basin that ends in a double (spanwise and vertical) convergence before entering the  
 198 channel. The total discharge and weir height are adjusted to set the water depth at  $H_w = 0.2$  m  
 199 and the upstream mean water velocity at  $U_0 = 0.05$  m s<sup>-1</sup>. The flow is then turbulent  
 200 (hydraulic diameter based Reynolds number  $Re_{Dh} = 2.7 \cdot 10^4$ , considering a kinematic viscosity  
 201 of water  $\nu = 10^{-6}$  m<sup>2</sup> s<sup>-1</sup>) and subcritical (Froude number  $Fr = 0.04$ ). Associated stem  
 202 Reynolds numbers, according to the average stem diameters of the different plants, are in the  
 203 range 90–360. The estimate of the length  $L_{dv}$  required for the flow development, using the  
 204 correlation (Eq. 5) proposed in Kirkgöz and Ardiçlioğlu (1997) is  $L_{dv} \approx 0.3$  m. The upstream  
 205 channel length  $L_u = 5$  m is significantly bigger than  $L_{dv}$ , and the flow is expected to be fully  
 206 developed before reaching the patch. The flume bed was composed of a mixture of sand and  
 207 gravel (grain size < 4 mm) to achieve more natural conditions in terms of sediment  
 208 characteristics and to facilitate parts of the experimental setup (e.g., placing the metal grid  
 209 with vegetation horizontally, inserting a force transducer in the sediment). The bed sediment  
 210 remained stable throughout the tests, including around the vegetation, and no scouring was  
 211 observed. Although real sediment was used to better represent natural conditions, a  
 212 quantification of sediment erosion/deposition patterns was not the objective of this work and  
 213 was not addressed.

## 214 2.2 Study species

215 In contrast to previous studies, which considered rigid or flexible plant mimics, we used  
 216 live vegetation to maintain realistic plant characteristics. The study species were *Callitriche*  
 217 *platycarpa* Kütz, *Groenlandia densa* (L.) Fourr. (sampled in a drainage channel of the Rhône  
 218 River, near Serrières-de-Briord, France, 45.8153° N, 5.4274° E) and *Vallisneria spiralis* L.  
 219 (sampled in a cut-off channel of the Rhône, 45.3401° N, 4.7760° E). Plant shoots were  
 220 attached on a perforated metal grid (0.75 m × 0.5 m length) that was directly placed in the  
 221 flume bed such that the grid had the same level of the bed. Sand was used to partly bury the  
 222 bottom grid and minimize any potential effects on the flow structure and on turbulence  
 223 generation. A plant shoot consists of a stem and leaves, but the size of the stem and leaves  
 224 (relative to each other) differs between the growth forms (Figure 2). For caulescent species  
 225 (*G. densa* and *C. platycarpa*), the stem is developed with long internodes. For rosette species  
 226 (*V. spiralis*), the stem is reduced and partly buried. Plants were arranged with a spacing  
 227 between shoots of  $3.15 \pm 0.36$  cm for *G. densa*,  $4.40 \pm 0.92$  cm for *V. spiralis* at high density,  
 228 and  $5.89 \pm 1.09$  cm for *V. spiralis* at low density (variability given as the mean ± SD of  $n = 3$



229 patches of different width). Due to the complex architecture of patches of *C. platycarpa*,  
 230 entire patches corresponding to the size required in the experiments were collected and  
 231 transplanted on the grid to preserve the patch structure. Therefore, the shoot density and  
 232 spacing for this species were determined at the end of the experiments by counting the  
 233 number of individuals. The spacing between shoots for this species was estimated to be  $0.97$   
 234  $\pm 0.20$  cm.



235  
 236 **Figure 2.** (A) *G. densa*, *C. platycarpa* and *V. spiralis* patches in the flume experiments; (B)  
 237 single plants of each species mounted on the force transducer during the drag measurements and (C) single  
 238 plants in the laboratory.

239 **Table 1.** Macrophyte species used in the flume experiments and description of their average  
 240 morphological characteristics and biomechanical traits [biomass per unit surface area (kg fresh mass  
 241 (FM)  $\text{m}^{-2}$ ); frontal area per canopy volume ( $a$ ,  $\text{m}^{-1}$ ), density (n. shoots  $\text{m}^{-2}$ ), Young's modulus  $E$   
 242 (MPa), second moment of area  $I$  ( $\text{m}^4$ ), flexural stiffness  $EI$  ( $\text{N m}^2$ )]. Variability in patch morphological  
 243 characteristics is given as the mean ( $\pm$  SD) of  $n = 3$  patches of different widths used in the  
 244 experiments. Biomechanical traits are the mean ( $\pm$  SD) of  $n = 10$  individuals per species.

Species	Patch morphological characteristics			Plant biomechanical traits			Total plant surface area ( $\text{m}^2$ )
	Biomass per unit surface area (kg FM $\text{m}^{-2}$ )	Frontal area per canopy volume ( $a$ , $\text{m}^{-1}$ )	Average density (n. shoots $\text{m}^{-2}$ )	$E$ (MPa)	$I$ ( $\text{m}^4$ )	$EI$ ( $\text{N m}^2$ )	
<i>G. densa</i>	1.31 $\pm$ 0.43	1.84 $\pm$ 0.41	1033 $\pm$ 231	42.05 $\pm$ 16.28	(5.25 $\pm$ 1.95) $\times 10^{-13}$	(2.11 $\pm$ 0.91) $\times 10^{-5}$	0.017 $\pm$ 0.002
<i>C. platycarpa</i>	2.14 $\pm$ 1.07	13.97 $\pm$ 6.77	11841 $\pm$ 5733	16.36 $\pm$ 0.14	(1.03 $\pm$ 0.58) $\times 10^{-13}$	(1.70 $\pm$ 1.23) $\times 10^{-6}$	0.011 $\pm$ 0.007
<i>V. spiralis</i> (High density)	1.57 $\pm$ 0.59	4.14 $\pm$ 1.78	567 $\pm$ 244	155.13 $\pm$ 137.41	(7.35 $\pm$ 4.82) $\times 10^{-14}$	(6.51 $\pm$ 2.56) $\times 10^{-6}$	0.014 $\pm$ 0.004
<i>V. spiralis</i> (Low density)	0.65 $\pm$ 0.23	2.27 $\pm$ 0.89	310 $\pm$ 221				

245

### 246 2.3 Measurements of morphological characteristics and biomechanical traits

247 The three species differ in morphology, biomechanical traits and density (Table 1). At the end  
 248 of the experiments, the patches were removed from the channel to measure their total fresh  
 249 mass. Based on the area covered by each patch, the fresh mass was expressed in kg of  
 250 biomass per unit surface area (kg fresh mass (FM)  $\text{m}^{-2}$ ), as shown in Table 1. The number of  
 251 individuals was used to calculate density (n. shoots per  $\text{m}^2$ ) and to estimate the spacing  
 252 between plant individuals  $\Delta S$ . The frontal area per canopy volume was calculated as  $a =$   
 253  $d/\Delta S^2$ , where  $d$  is the stem diameter (for *G. densa* and *C. platycarpa*) or leaf width (for *V.*  
 254 *spiralis*), and  $\Delta S$  is the average spacing between plant individuals in the patch (Nepf, 2012).  
 255 The stem diameter and leaf width were measured in 10 individuals per species using a digital  
 256 calliper and were on average 1.79  $\pm$  0.16 mm for *G. densa*, 1.18  $\pm$  0.14 mm for *C. platycarpa*,  
 257 and 7.28  $\pm$  1.10 mm for *V. spiralis*. The solid volume fraction occupied by the canopy  
 258 elements,  $\phi$ , was also calculated. For *G. densa* and *C. platycarpa*, with a circular stem cross-  
 259 section,  $\phi \approx (\pi/4)ad$ . For *V. spiralis*, with strap-like linear leaves of width  $d$  and thickness  $b$ ,  $\phi$   
 260  $= db/\Delta S^2$ .

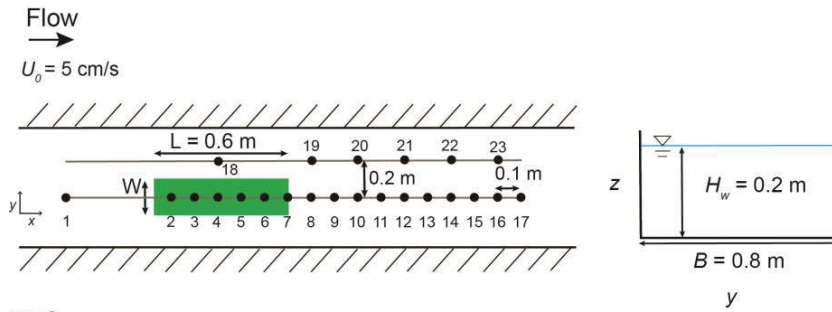
261 Biomechanical traits were measured through bending tests on 10 replicate individuals  
 262 per species using a universal testing machine (Instron 5942, Canton, MA, USA). Mechanical  
 263 forces act on the stems of species with a caulescent growth form, such as *G. densa* and *C.*

264 *platycarpa*, while the forces concentrate on leaves for species with a rosette growth form,  
265 such as *V. spiralis* (Hamann & Puijalon, 2013). Therefore, bending tests were performed on  
266 the basal part of the main stem of *G. densa* and *C. platycarpa* and on a single leaf of *V.*  
267 *spiralis*. Because we are working on flexible vegetation, the bending Young's modulus and  
268 flexural stiffness were chosen because they are relevant for the reconfiguration properties of  
269 the plants (Table 1).

270 Three-point bending tests were performed on leaf samples of *V. spiralis*. This test  
271 consists of a force applied at a constant rate of  $10 \text{ mm min}^{-1}$  at the midpoint of a sample  
272 placed on two supports (Silinski et al., 2018) with a support span of 60 mm. Due to the high  
273 flexibility of stems of *G. densa* and *C. platycarpa*, a three-point bending test could not be  
274 performed on these species. The samples were tested as cantilever beams using a one-fixed  
275 end bending test (Hamann & Puijalon, 2013), where each basal stem sample (5 cm in length)  
276 was clamped horizontally at its basal end while a force was applied at the midpoint of the  
277 sample by lowering a probe at a constant rate of  $10 \text{ mm min}^{-1}$ .

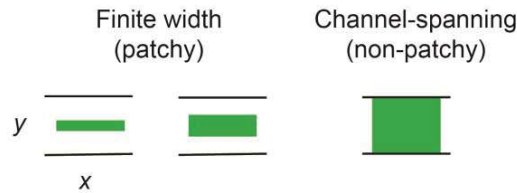
278 The following biomechanical traits were calculated: (1) the bending Young's modulus  
279 ( $E$  in MPa) quantifies the sample stiffness, and is defined as the slope of a sample's stress-  
280 strain curve in the elastic deformation region; (2) the second moment of area ( $I$  in  $\text{m}^4$ )  
281 quantifies the distribution of material around the axis of bending, accounting for the effect of  
282 the cross-sectional geometry of a structure on its bending stress. Because the stem cross  
283 section for *G. densa* and *C. platycarpa* was circular,  $I$  was calculated as  $I = (\pi r^4)/4$ , where  $r$  is  
284 the radius of the stem cross section (Niklas, 1992). Because the cross-sectional geometry of  
285 leaves of *V. spiralis* was triangular,  $I$  was calculated as  $I = (bh^3)/36$ , where  $b$  and  $d$  are the  
286 base and height of a triangle based on the sample leaf width and thickness; (3) the flexural  
287 stiffness ( $EI$  in  $\text{N m}^2$ ) was calculated by multiplying  $E$  and  $I$ , and quantifies the resistance to  
288 bending (stiffness) of the stem or leaf fragment. A linear mixed model using maximum  
289 likelihood was used to test for differences in biomechanical traits across species. This model  
290 included species as the fixed effect and one random effect of individual plants (to account for  
291 non-independence between the plants sampled within the same patch). The dependent  
292 variables were Young's modulus, second moment of area and flexural stiffness.

A) ADV profile measurements

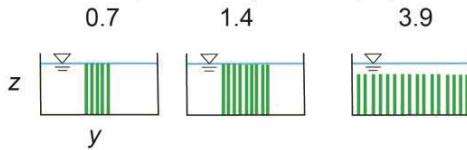


B) Cases

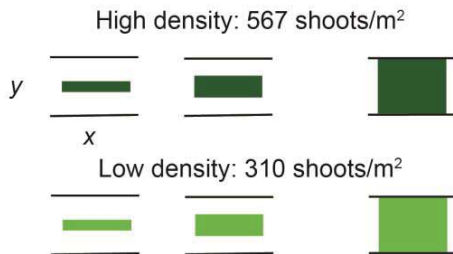
1. Spatial configuration



2. Patch aspect ratio (width/height)



3. Density



293

294 **Figure 3.** Schematic representation of the experimental channel and cases. **a)** Top view of the channel  
 295 (with the vegetation patch shown in green) and schematic view of the channel cross-section.  
 296 Numbered black dots indicate the location of flow velocity profiles measured with a Vectrino II  
 297 Acoustic Doppler Velocimeter (ADV). Diagram not drawn to scale. **b)** Overview of experimental  
 298 cases with varying spatial configurations, patch aspect ratios and patch densities. Note the channel-  
 299 spanning case with the flow passing above the canopy (submerged) and finite-width cases where the  
 300 submerged canopy can locally reach the free surface. Throughout this study, the incoming flow  
 301 Reynolds number (based on the hydraulic diameter) is approximately 27000.

302

303 2.4 Patch dimensions

304 As shown in Figure 3b and Table 2, we compared a channel-spanning patch and two  
 305 finite patches of different widths and thus the aspect ratio ( $W/h$ ). For one species (*V. spiralis*),

306 we tested the effect of shoot density by removing approximately half of the shoots from each  
307 patch. Because of co-variation between different patch properties (i.e., density also changes  
308 with patch size), there is an overlap in the range of densities in the high- and low-density  
309 cases (but not in terms of biomass per unit surface area). Thus, the density effects are  
310 analysed as paired comparisons between the two cases for one given patch size. The shoot  
311 density could not be kept constant across all species primarily due to differences in biomass  
312 per shoot, which would have led to unrealistic patch characteristics. Other characteristics  
313 differ between species (e.g., biomechanical traits, morphology, biomass distribution along the  
314 stem). Thus, the choice was made to use realistic patch architecture and densities per species  
315 to recreate how they grow in natural conditions and to study density effects only within the  
316 same species.

317 The undeflected plant length ranged from 8–48 cm for *G. densa*, 4–45 cm for *C.*  
318 *platycarpa*, and 7–43 cm for *V. spiralis* (Table 2). Such a large range is expected for natural  
319 patches due to the differences in plant size between the plants in the front and rear of the  
320 patch. The patch height in this study is defined as the deflected vegetation height ( $h$ ).  
321 Sideview pictures of the patches could not be taken because there was no transparent opening  
322 on the side of the outdoor flume. Using only three species also prevented us from performing  
323 quantitative analyses to compare plant deflection with the biomechanical traits. The channel  
324 blockage factor of the patch (i.e., the share of the channel cross-section occupied by the  
325 patch) was measured for all cases using underwater photographs. This parameter is relevant  
326 because the flow forced through the patch may increase with increasing channel blockage,  
327 affecting the wake length (Zong & Nepf, 2012).

## 328 2.5 Flow velocity and turbulence measurements

329 Flow velocity profiles were measured using an Acoustic Doppler Velocimeter (ADV), the  
330 Nortek Vectrino II profiler with a down-looking probe. The Vectrino II was used to measure  
331 the profile in 5 bins with a 3.5-cm sample length and cell size of 0.1 cm over 3 minutes at 100  
332 Hz, to cover the depth from 0 cm from the bed to 16 cm; the top part of the flow could not be  
333 measured by the profiler due to the down-looking probe. To minimize the bed interference on  
334 the velocity measurements, only the cells located in the upper 1.5 cm were used in the  
335 calculations for the bottom part of the profile (0–3.5 cm from the bed).

336 Profiles were measured 1 m upstream of the vegetation patch ( $U_0$ ). As shown in Figure  
337 3a, 5 profiles were measured in the vegetation canopy (points 2–6, every 10 cm) along the  
338 patch centreline, one profile (point 7) at the downstream edge and 10 profiles downstream of  
339 the vegetation (points 8–17, every 10 cm). To minimize interference by vegetation structures  
340 within the sampling volume of the ADV probe and in the space between the probe and the  
341 sampling volume, the stems were moved aside, while the probe started at the lowest  
342 measuring point for each vertical profile within the vegetation. This process prevented the  
343 canopy from being compressed as the probe moves towards the bed (Cornacchia et al., 2019).  
344 At each ADV measurement position in the vegetation, the canopy height was measured using  
345 a tape measure. This method was preferred over point gauge measurements due to the  
346 continuous movement of the plants with the current, leading to a measurement uncertainty of

347 a few centimetres. Because patches of flexible macrophytes generally exhibit a gradual  
 348 increase in patch height along their length (green dashed lines in Figure 4; Licci et al., 2019),  
 349 both the mean and maximum patch heights are reported in Table 1. The downstream edge of  
 350 the vegetation patch was identified as the end of the canopy overhanging the bed and not as  
 351 the end of the rooted part.

352 Lateral profiles were measured along a line located 20 cm to the side of the patch  
 353 centreline, and 20 cm from the flume wall. Along this line, one profile was measured halfway  
 354 along the canopy length  $L$  (point 18 in Figure 3a), and 5 profiles were measured downstream  
 355 of the canopy (every 20 cm; points 19–23 in Figure 3a). The velocity increase (in percent) at  
 356 the lateral side of the patch was calculated as the difference between the depth-averaged  
 357 velocity in profile 18 (located 20 cm to the side of the patch centreline) and the incoming  
 358 depth-averaged upstream velocity  $U_0$ , divided by the upstream velocity.

359 Data processing was performed in MATLAB. To ensure that measurements were based on  
 360 reliable data points, low-quality data points (i.e., correlation below the standard quality  
 361 threshold of 70% and signal-to-noise ratio (SNR) below 15 dB) were removed during  
 362 postprocessing. Data were despiked using the method described by Goring and Nikora (2002)  
 363 and analysed to calculate time-averaged mean velocities. The instantaneous velocities  
 364 ( $u(t), v(t), w(t)$ ) measured in the streamwise, lateral, and vertical directions, respectively,  
 365 were separated into time averages ( $\bar{U}, \bar{V}, \bar{W}$ ), and instantaneous turbulent fluctuations  
 366 ( $u'(t), v'(t), w'(t)$ ) (e.g. as  $u'(t) = u(t) - \bar{U}$ , and similarly for  $v$  and  $w$ ). The total turbulent  
 367 kinetic energy (TKE,  $\text{m}^2 \text{s}^{-2}$ ) was calculated as  $TKE = \frac{1}{2} (\overline{u'^2} + \overline{v'^2} + \overline{w'^2})$ .

368 In this study, the steady wake length is characterized in two different ways. The first  
369 definition,  $L_{w1}$ , indicates the most downstream distance (up to  $x/L = 2.6$ ) where the  
370 streamwise velocity is diminished to more than half of the incoming velocity ( $u < 0.5U_0$ ),  
371 anywhere on the vertical profile, following Boothroyd et al. (2017). The second definition,  
372  $L_{w2}$ , is estimated to be the distance downstream of the patch before the depth-averaged  
373 velocity along the patch centreline begins to increase, as shown in Figure 1a, and denotes the  
374 distance from the patch downstream edge to the position of minimum velocity (Liu et al.,  
375 2018). This definition was chosen as it corresponds to the location where momentum injected  
376 by turbulent structures from outside accelerates the flow in the wake, marking the end of the  
377 zone sheltered by the canopy; however, defining the start of the velocity increase can be  
378 difficult, especially with a limited number of measurements. Hence, we also considered  $L_{w1}$   
379 as an alternative, more systematic definition of the wake. In the cases where there was no  
380 clear minimum in depth-averaged velocity downstream of the patch,  $L_{w2}$  was assumed to be  
381 lower than the 0.1-m spacing between the downstream edge of the patch and the first  
382 downstream velocity profile and was therefore set to 0.05 m. This estimation of the length of  
383 the steady wake region does not account for the recovery region in which the velocity  
384 increases up to the original value upstream of the patch. This choice was made to assess the  
385 sheltering effect in a region of both reduced velocity and turbulence intensity, as opposed to  
386 the recovery region where an increase in centreline velocity and turbulence are observed (Liu  
387 et al., 2018).

## 388 2.6 Drag force measurements

389 Drag forces were measured at points 7–17 (Figure 3a) using a custom-made force  
390 transducer (Doerler-Mesures SAS, Vandœuvre-lès-Nancy, France) that consisted of a metal  
391 foil strain gauge force transducer (single-point load cell) that measured forces in one  
392 direction with an uncertainty of  $\pm 0.05$  N. A base with a hole fitting the size of the transducer  
393 was placed in the channel bed so that the transducer placed in the hole had its top part at the  
394 same level of the channel bed. Each plant was mounted on the transducer (after elimination of  
395 belowground parts) and fixed with plastic paraffin film (Figure 2b). Drag forces were  
396 measured for 1 minute at 100 Hz. Drag measurements in some downstream locations were  
397 taken for velocities near zero. Thus, these measurements should be interpreted with care due  
398 to interference with opposing forces due to mounting of the plant on the drag sensor. Because  
399 it is impossible to mount shoots perfectly straight upwards on the drag sensor, any deviation  
400 from perfectly vertical will cause the buoyancy of the plant itself to impose a small force on  
401 the drag sensor (Bal et al., 2011). Similar considerations held for mounting the sensor on the  
402 bed due to local irregularities and grain size. To compare between species, drag was  
403 expressed as a function of the total plant surface area (Table 1). Therefore, the total surface  
404 area was obtained for each plant at the end of the drag measurements. The individual leaves  
405 and stems were separated, scanned and measured using WinFOLIA software (Regent  
406 Instruments Inc.). The total surface area was described by the sum of all plant parts. Drag  
407 measurements were performed on a set of two replicate plants of the same species to ensure  
408 consistency (one set for *G. densa*, one set for *C. platycarpa*, one set for *V. spiralis* high-

409 density and one for *V. spiralis* low-density). The plants used for drag measurements had a  
 410 size comparable to the size of the individual plants of the patch (Figure 2c).

411 The drag force per unit surface area is expected to be proportional to  $U^2$  (for rigid  
 412 vegetation) or  $U^{(2+\chi)}$  (for flexible vegetation), where  $U$  is the approach velocity and  $\chi$  is the  
 413 Vogel exponent (Vogel, 1984; Västilä & Järvelä, 2014; Gosselin, 2019). For very flexible  
 414 vegetation that reconfigures into streamlined shape, this exponent is often negative, with  $\chi \sim$   
 415  $-1$ , so that an approximately linear increase of drag with flow velocity ( $U^l$ ) can be expected  
 416 as a good fit to the data (De Langre et al., 2012). Negative values of the Vogel exponent,  
 417 ranging between  $-1.2$  and  $-0.3$ , were found in previous studies (Vogel, 1984; Schutten &  
 418 Davy, 2000; Puijalón et al., 2005; Sand-Jensen, 2008; Bal et al., 2011). Thus, a linear  
 419 relationship between drag and velocity is expected in this study due to the use of highly  
 420 flexible and isolated plants. This relationship is tested with Pearson's correlation coefficient.

### 421 3 Results

#### 422 3.1 Between-species comparisons of biomechanical traits

423 Results showed significant differences in biomechanical traits of the investigated species  
 424 (Table 1) in terms of Young's modulus (ANOVA,  $F_{2,6} = 6.93$ ,  $p = 0.03$ ) and flexural stiffness  
 425 (ANOVA,  $F_{2,6} = 32.47$ ,  $p < 0.001$ ). The Young's modulus of *V. spiralis* was significantly  
 426 higher than that of *G. densa* and *C. platycarpa* (Tukey's HSD  $p < 0.02$  for both pairwise  
 427 comparisons). *G. densa* had the stiffest stems, with a significantly higher flexural stiffness  
 428 than the other two species (Tukey's HSD  $p < 0.001$  for all pairwise comparisons) and the  
 429 highest second moment of area among the species (ANOVA,  $F_{2,6} = 31.53$ ,  $p < 0.001$ ). *C.*  
 430 *platycarpa* had the highest flexibility and lowest flexural stiffness of all three species.

#### 431 3.2 Flow patterns around the reconfigured vegetation

432 Figure 4 shows the heights of the vegetation canopy along with plots of streamwise  
 433 and vertical velocities for the three vegetation configurations for each species. Because real  
 434 plants were used, the deflected height was not controlled in the experiments. For all species  
 435 and all cases, the canopy exhibited reconfiguration and particularly bending of the plants.  
 436 Undeflected plant lengths were indeed longer than the water depth (Table 2). Plant bending  
 437 decreases (the patch height increases) downstream due to the sheltering effect of upstream to  
 438 downstream plants (Barsu et al., 2016). Despite their bending, plants were sufficiently long to  
 439 still reach the water surface for finite-width cases ( $\max(h/H_w) = 1$ ). This is consistent with  
 440 field conditions, where most species in shallow waters grow just below or on the water  
 441 surface: the submergence ratio  $h/H_w$  gradually increases with increasing patch length,  
 442 reaching values near 1 (Licci et al., 2019). Conversely, the plants remained below the water  
 443 surface for channel-spanning cases ( $\max(h/H_w) = 0.8-0.9$ , depending on the species). The  
 444 channel blockage factor was similar between the two finite-width cases (Supporting  
 445 Information Figure S1). The small difference in blockage factors between the two cases  
 446 results from adjustments of the patch where an increase in width was buffered with a  
 447 decrease in height; we observed less bending of the plants in the narrowest patch, except for  
 448 *G. densa* (cf. patch height and undeflected plant length in Table 2).



449 The changes in deflected plant height and channel blockage are related to differences  
 450 in the velocity field. For all species, the flow velocity within the vegetation was lower than  
 451 that of the incoming flow. However, due to the blockage effect in the channel-spanning case,  
 452 the flow was deviated by the vegetation patch towards a water layer of high velocity observed  
 453 on top of the canopy, while the water flow within the canopy was considerably slow (less  
 454 than half of the incoming depth-averaged velocity). As expected, this high-velocity water  
 455 layer observed in the channel-spanning case disappeared in the two finite-width patch cases  
 456 as the canopy reached the water surface ( $h/H_w = 1$ ), as shown in Figure 4 by the green dashed  
 457 line depicting the patch shape. This phenomenon leads to differences in the vertical velocities  
 458 observed within the patch; nearly absent in the channel-spanning case, downwards velocities  
 459 are observed within the finite-width patches – depicted in Figure 4 by the downward vectors  
 460 for  $x/L < 1$ , except for *C. platycarpa* – where the flux is directed towards the bed where the  
 461 canopy is marginally less dense. In the two finite patch cases, the velocity increased at the  
 462 lateral sides of the patch, characterized by the measurement along profile 18 (Figure 3a) 0.2  
 463 m from the centreline. This increase (Figure 6) reached on average 111% compared to the  
 464 incoming depth-averaged velocity (profile 1) for *G. densa*, 83% for *C. platycarpa*, and 86%  
 465 for *V. spiralis* in the high-density case and 82% in the low-density case. Differences between  
 466 spanning and non-spanning cases were also present in the wake, downstream of the patch.  
 467 The channel-spanning case exhibited vertical heterogeneity in the flow velocity profiles  
 468 downstream of the vegetation, with faster flow in the upper part of the water column and  
 469 attenuated flow near the bed. This is consistent with a relatively low TKE in the wake (Figure  
 470 5), except in the upper part corresponding to the boundary between the wake and the upper  
 471 free flow, where the highest values of  $-\rho \overline{u'w'}$  Reynolds stresses were incidentally observed  
 472 (Supporting Information Figure S2). The wake closed rather by momentum injected in the  
 473 wake from the rapid flow above. In contrast, in the finite-width patch cases, the vertical  
 474 velocity profiles in Figure 4 did not exhibit two layers, with low streamwise velocity  
 475 throughout the water column. Again, this is consistent with the TKE measurements (Figure  
 476 5). The bleeding flow through the non-spanning canopy produced high, quite uniform, levels  
 477 of TKE in the second half of the canopy and the whole wake, as observed by Chang and  
 478 Constantinescu (2015). Relatively strong vertical velocities were observed just downstream  
 479 of the patch for the particular case of *V. spiralis*, which might arise from the combined effect  
 480 of its plant architecture and the plant bending near the bed, similar to the vertical velocities  
 481 appearing when an emerging cylinder is inclined from the normal direction to the bottom  
 482 (Kitsikoudis et al., 2017). The streamwise velocity however increased with longitudinal  
 483 distance from the canopy edge. The highest levels of  $-\rho \overline{u'v'}$  Reynolds stresses were observed  
 484 (Supporting Information Figure S3), characterizing a momentum injected by eddies in the  
 485 wake from the lateral free flows, consistently with the separated shear layers observed on the  
 486 sides of patches of cylinders by Chang and Constantinescu (2015).

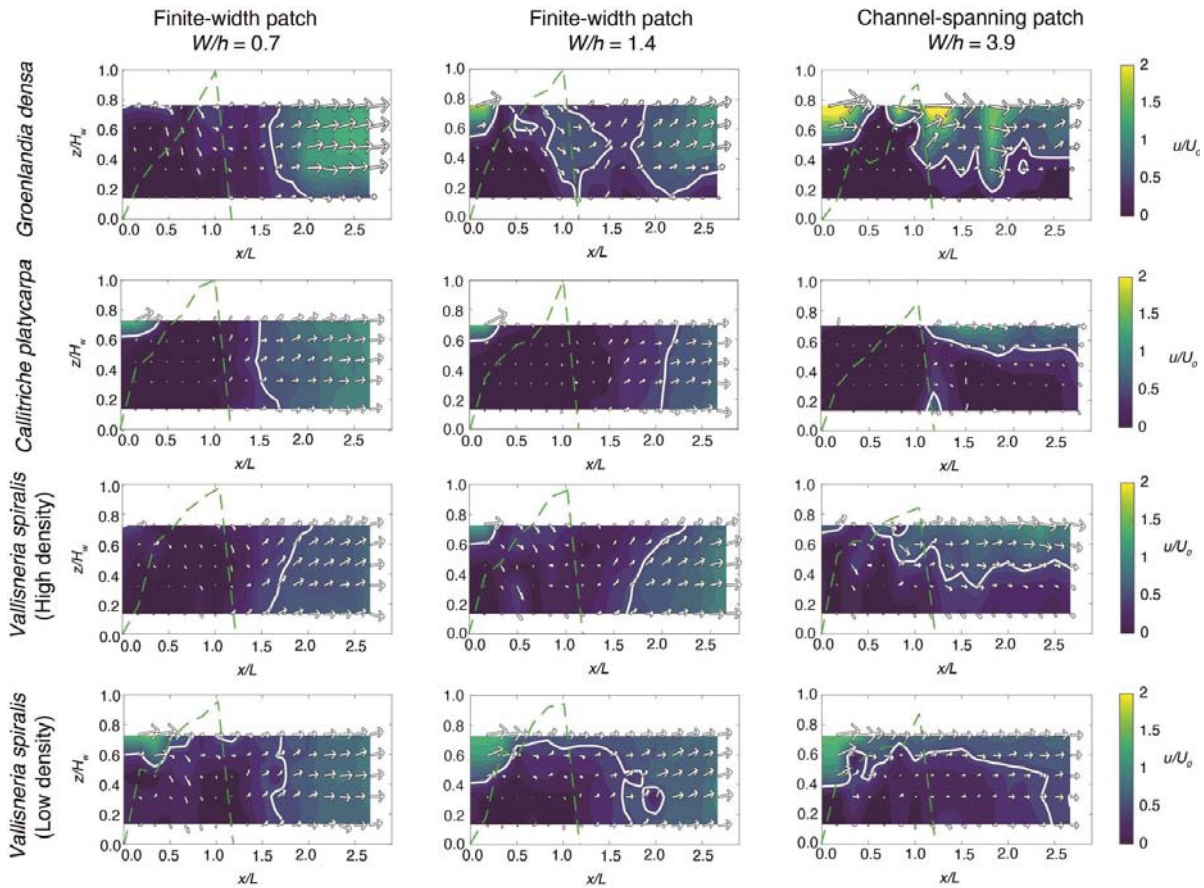
487 Figure 6 shows the evolution of the depth-averaged velocity downstream of the patch  
 488 in two vertical planes, in the middle of the channel (centreline profile) and 0.2 m aside  
 489 (lateral profiles). The overall conclusions are similar to those based on velocities along the  
 490 vertical profile. As expected for the non-spanning case, lateral profiles exhibited higher  
 491 velocities than centreline profiles due to the obstruction effect; this effect is absent in the

492 channel-spanning case, while profiles are not strictly identical. The centreline depth-averaged  
493 velocity increased more rapidly to recover  $U_0$  for the narrowest patch, which is consistent  
494 with the closing of the steady wake. The influence of the patch density appears negligible on  
495 the centreline profiles, but the stronger acceleration on the laterals was stronger for the denser  
496 patch of *V. spiralis*, at least for the widest non-spanning patch.

497 **Table 2.** Summary of experimental cases and results. Patch length (L) is 0.60 m for all cases. The undeflected plant length was measured on a  
 498 sample of 10 plants per case.

Case	Species	Patch width W (m)	Mean patch height (m) $\pm$ SD	Max. patch height h (m)	Undeflected plant length (m)	Patch aspect ratio (W/L)	Patch aspect ratio (W/h)	Water height $H_w$ (m)	Patch density (n. shoots $m^{-2}$ )	Solid volume fraction ( $\phi$ )	Length of steady wake $L_{w1}$ (m)	Length of steady wake $L_{w2}$ (m)
GRO1	<i>G. densa</i>	0.15	0.12 $\pm$ 0.06	0.21	0.26 $\pm$ 0.12	0.25	0.71	0.21	1267	0.003	0.60	0.20
GRO2	<i>G. densa</i>	0.30	0.15 $\pm$ 0.05	0.21	0.21 $\pm$ 0.11	0.50	1.43	0.21	1028	0.003	> 1.0	0.40
GRO3	<i>G. densa</i>	0.75	0.11 $\pm$ 0.06	0.19	0.21 $\pm$ 0.05	1.25	3.95	0.21	804	0.002	> 1.0	0.40
CAL1	<i>C. platycarpa</i>	0.15	0.16 $\pm$ 0.05	0.22	0.21 $\pm$ 0.08	0.25	0.68	0.22	8133	0.009	0.40	0.05
CAL2	<i>C. platycarpa</i>	0.30	0.14 $\pm$ 0.05	0.23	0.24 $\pm$ 0.12	0.50	1.30	0.23	8946	0.010	0.70	0.10
CAL3	<i>C. platycarpa</i>	0.75	0.14 $\pm$ 0.05	0.20	0.25 $\pm$ 0.08	1.25	3.75	0.23	18445	0.021	> 1.0	0.70
VAL1	<i>V. spiralis</i>	0.15	0.16 $\pm$ 0.07	0.21	0.26 $\pm$ 0.10	0.25	0.71	0.22	833	0.004	0.60	0.05
VAL2	<i>V. spiralis</i>	0.30	0.16 $\pm$ 0.05	0.21	0.28 $\pm$ 0.10	0.50	1.43	0.22	511	0.003	0.70	0.10
VAL3	<i>V. spiralis</i>	0.75	0.16 $\pm$ 0.03	0.19	0.28 $\pm$ 0.09	1.25	3.95	0.22	356	0.002	> 1.0	0.10
VAL4	<i>V. spiralis</i>	0.15	0.14 $\pm$ 0.04	0.21	0.24 $\pm$ 0.09	0.25	0.71	0.22	444	0.002	0.40	0.05
VAL5	<i>V. spiralis</i>	0.30	0.15 $\pm$ 0.06	0.21	0.28 $\pm$ 0.10	0.50	1.43	0.22	278	0.001	0.60	0.10
VAL6	<i>V. spiralis</i>	0.75	0.14 $\pm$ 0.03	0.19	0.28 $\pm$ 0.09	1.25	3.95	0.22	209	0.001	0.90	0.40

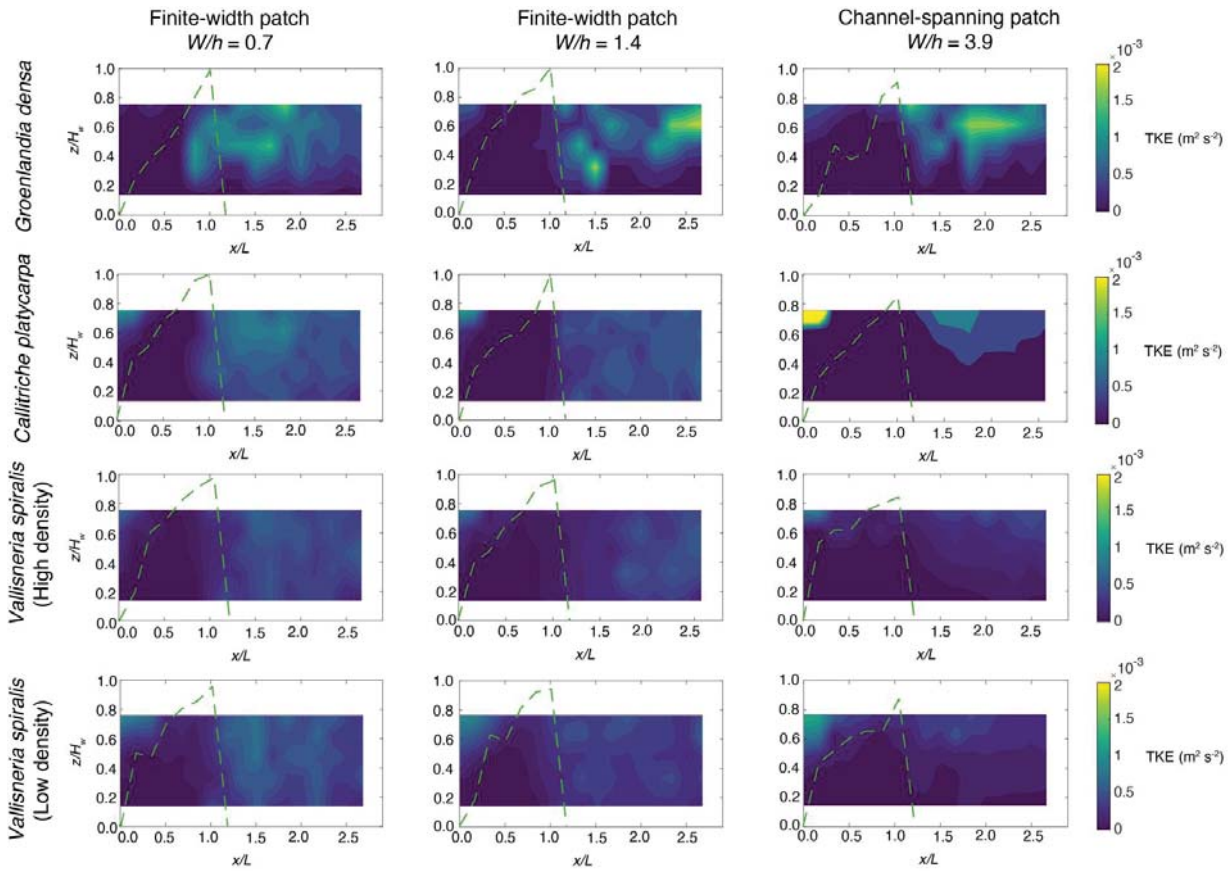
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502  
503

**Figure 4.** Resultant vector plots of streamwise and vertical velocities in the longitudinal direction. For each species, three configurations with different patch  $W/h$  ratios were considered. Green dashed lines indicate the height of the vegetation canopy. The white isoline denotes locations where the local streamwise velocity  $u < 0.5U_0$ . The longitudinal distance ( $x/L$ ) is normalized by the patch length  $L$  (60 cm for all configurations).

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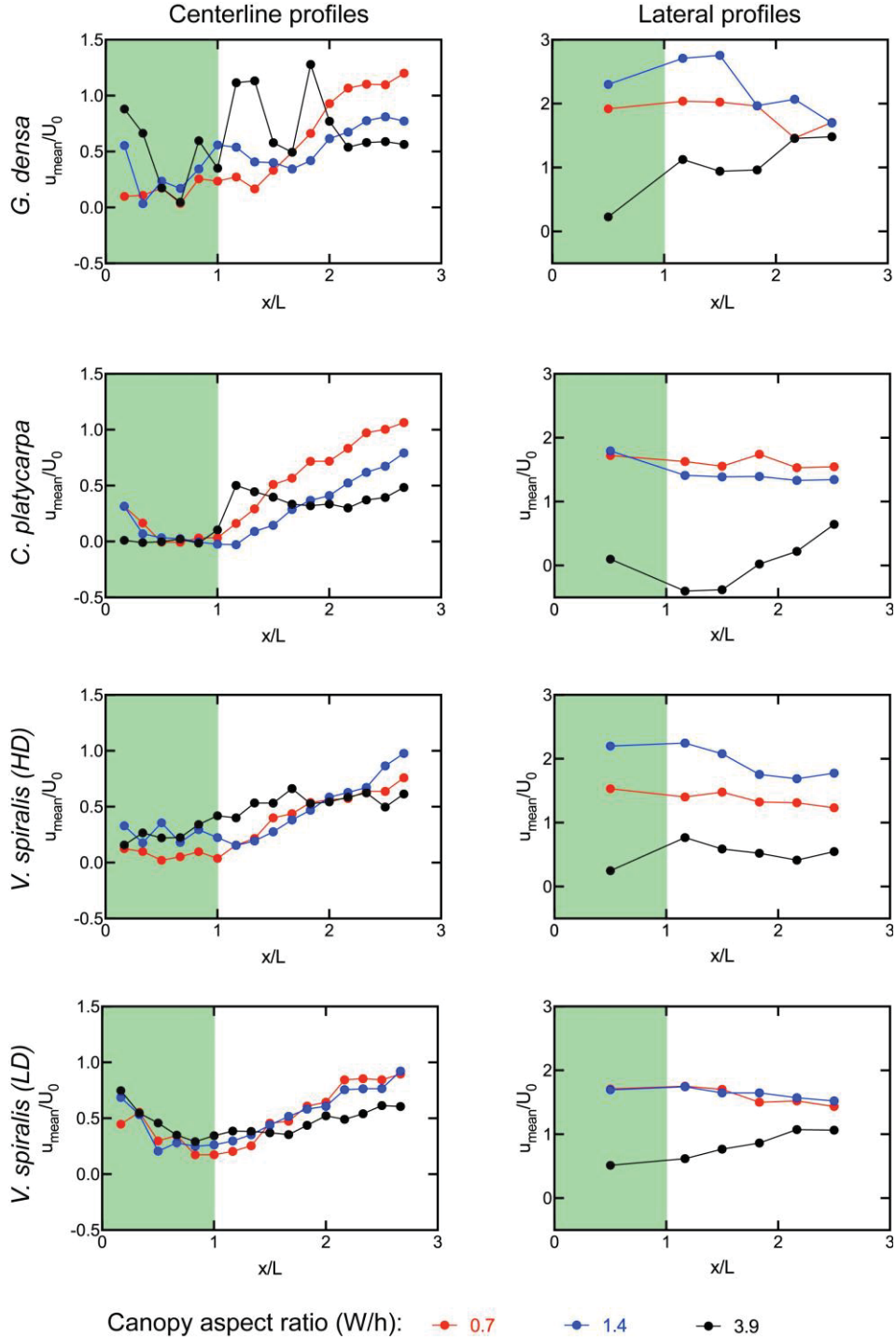


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**Figure 5.** Colormap plots of the turbulent kinetic energy (TKE) in the central, vertical, streamwise plane. For each species, three configurations with different patch  $W/h$  ratios were considered. Green dashed lines indicate the height of the vegetation canopy.



512 **Figure 6.** Longitudinal profiles of normalized depth-averaged velocity ( $u_{\text{mean}}/U_0$ ) along the centreline and on  
 513 the side of vegetation patches of *Groenlandia densa*, *Callitriche platycarpa* and *Vallisneria spiralis* (High and  
 514 low density). The longitudinal distance ( $x/L$ ) is normalized by the patch length  $L$  (60 cm for all  
 515 configurations). The green shaded area indicates the location of the vegetation patch.  
 516

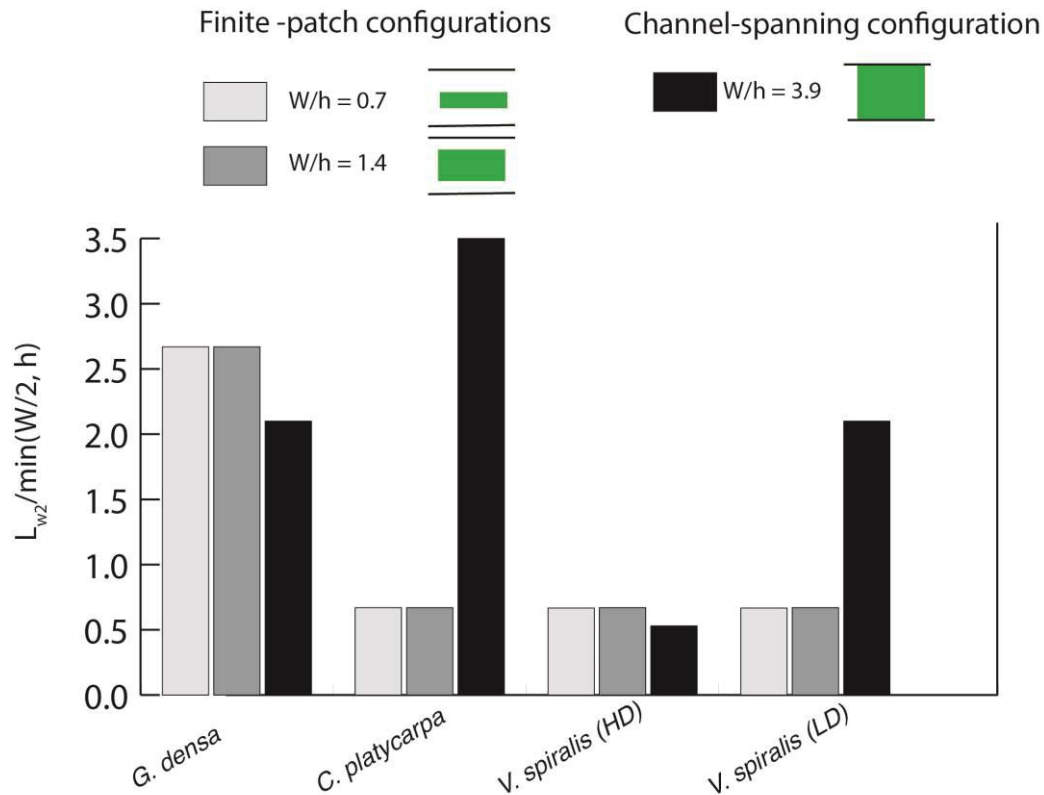
### 517 3.3 Steady wake length

518 The steady wake  $L_{wl}$  is analysed directly from Figure 4. For all species, in the channel-spanning  
 519 case,  $L_{wl}$  extended to more than 2.5 patch lengths (from the patch leading edge), longer than for

520 the non-spanning cases, which is consistent with the blocking effect and a 2D momentum  
 521 transfer from the flow above the canopy towards the bed (Figure 4). In four out of twelve cases,  
 522  $L_{w1}$  was longer than assumed a priori and was not fully resolved by the measurements  
 523 (Supporting Information Figure S4). For *V. spiralis*, the wake was shorter near the bed. The  
 524 rosette growth form of this species associated with a high density promoted the flow near the  
 525 bed. This is similar to what was observed for such rosette plant species (*T. latifolia*; Xu and Nepf  
 526 (2020)) or for isolated plants with narrow trunks near the bed, in terms of the time-averaged  
 527 vertical velocity profile (Kitsikoudis et al., 2016) or wake shape (Boothroyd et al., 2017) under  
 528 laboratory conditions. This rosette growth form effect, or more generally plant architecture  
 529 effects, might combine with the plant bending effect near the bed, consistently with Kitsikoudis  
 530 et al. (2017) where such a wake shortening near the bed was observed, jointly with the  
 531 appearance of vertical velocities, for an impervious inclined cylinder. Conversely, for the three  
 532 other non-spanning cases,  $L_{w1}$  was longer near the bed because the porosity was not decreased  
 533 there, due to the plant structure (Figure 2; *C. platycarpa*, *G. densa*). For reference, in the profile  
 534 without plants (1 m upstream of the patch), the bottom 1.9 cm of the profile had a streamwise  
 535 velocity  $u < 0.5U_0$ .

536 Figure 7 shows the wake length  $L_{w2}$ , and the associated results are summarized in Table  
 537 2. Previous studies showed that the steady wake length is approximately equal to the patch width  
 538 when  $W < h$ , or to the patch height when  $W > h$  (Hu et al., 2018; Liu et al., 2018). Therefore, to  
 539 make the wake lengths nondimensional, all wake lengths in Figure 7 were normalized by the  
 540 canopy half-width ( $W/2$ ) for configurations where  $W/2 < h$  and by canopy height ( $h$ ) for cases  
 541 where  $W/2 > h$ . Within each species, measurements showed a difference between channel-  
 542 spanning and finite-width patch configurations, with the dimensionless wake length  
 543  $L_{w2}/\min(W/2, h)$  being higher for  $W/h = 3.9$ , at least for two species. Conversely, within each  
 544 species, the dimensionless steady wake length appears not to depend on the aspect ratio  $W/h$  for  
 545  $W/h \leq 1.4$ . Between species, in the channel-spanning patch, the dimensionless steady wake length  
 546 exhibited high variability. For finite-width patch configurations, results were more homogeneous  
 547 between species, except for *G. densa*. In the finite-width configurations, increasing shoot density  
 548 did not significantly modify the length of the wake region for *V. spiralis* (Figures 6 and 7).  
 549 However, for the channel-spanning patch, decreasing shoot density extended the steady wake  
 550 length  $L_{w2}$  (Figures 6 and 7).

551 When comparing the two different definitions of steady wake length, relatively stable  
 552 patterns emerge. According to both definitions, *G. densa* is the species that produced the longest  
 553 steady wake region, and little difference in steady wake length was observed among the other  
 554 three cases (Figure 6; Supporting Information Figure S4). Therefore, although the steady wake  
 555 length quantified according to  $L_{w1}$  is generally longer, there is consistency across the two  
 556 definitions.



557  
 558 **Figure 7.** Dimensionless wake length (i.e., normalized by the smallest dimension between patch half-  
 559 width and max. height) in the channel-spanning and two finite-patch configurations for three macrophyte  
 560 species (*Groenlandia densa*, *Callitriche platycarpa* and *Vallisneria spiralis*) defined as the zone upstream  
 561 of reacceleration ( $L_{w2}$ ).

### 562 3.4 Drag force measurements

563 Figure 8 shows the measured drag force per total surface area in the wake ( $\text{N m}^{-2}$ ) as a function  
 564 of the corresponding normalized depth-averaged streamwise velocity ( $u_{\text{mean}}/U_0$ ) at a given  
 565 downstream location, taken at the same location of the drag force measurement. The 5%  
 566 maximum values and variance in the measurements are summarized in more detail in the  
 567 Supporting Information (Table S1). Negative drag forces at the lowest velocity are due to the  
 568 weight of the plant itself imposing a small force on the drag sensor, which is related to the  
 569 difficulty of mounting a shoot perfectly vertical on the drag sensor.

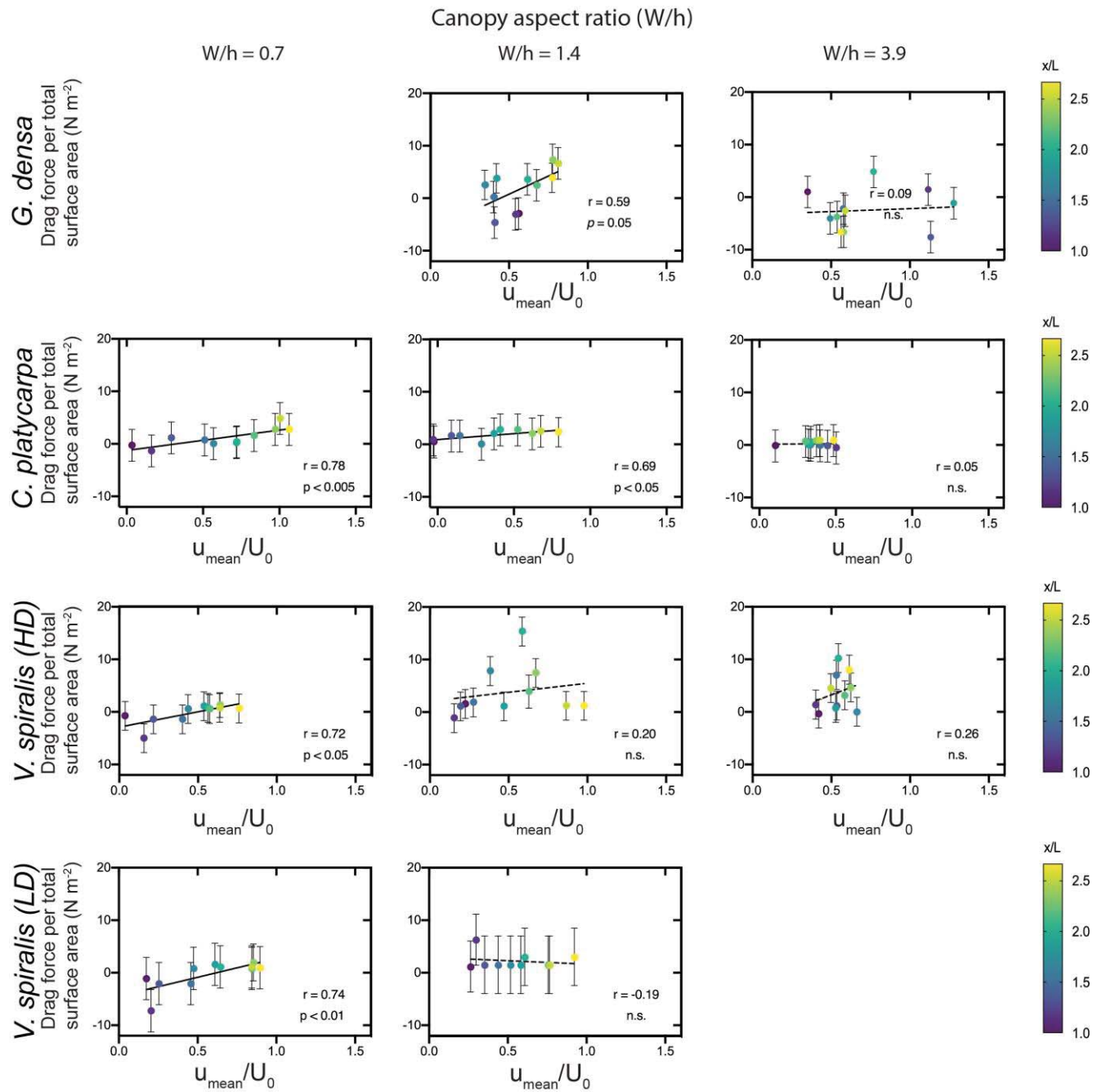
570 Measurements for two of the three species (*G. densa* and *C. platycarpa*) indicate that  
 571 drag reduction is related to downstream flow modification in the case of finite-width patches but  
 572 not for channel-spanning patches. We found a significant correlation between drag forces and  
 573 flow velocities downstream of the vegetation for the two finite-width patches of *G. densa*  
 574 (Pearson's correlation coefficient  $r = 0.59$ ,  $p = 0.05$  for  $W/h = 1.4$ ) and *C. platycarpa* ( $r = 0.78$ ,  
 575  $p < 0.005$  for  $W/h = 0.7$ ;  $r = 0.69$ ,  $p < 0.05$  for  $W/h = 1.4$ ). For high- and low-density *V. spiralis*  
 576 canopies, we found a significant correlation between drag forces and downstream flow velocities  
 577 for the finite-width patch configuration where  $W < h$  ( $r = 0.72$ ,  $p < 0.05$  for the high-density



578 patch;  $r = 0.74$ ,  $p < 0.01$  for the low-density patch) but not for the finite-width patch where  $W > h$   
579 ( $r = 0.20$ ,  $p = 0.55$  for the high-density patch;  $r = -0.18$ ,  $p = 0.6$  for the low-density patch).

580 In the channel-spanning configurations ( $W/h = 3.9$ ), we did not observe a significant  
581 correlation between drag forces and flow velocities at a given downstream location in any of the  
582 three species ( $r = 0.09$ ,  $p = 0.79$  for *G. densa*;  $r = 0.05$ ,  $p = 0.9$  for *C. platycarpa*;  $r = 0.33$ ,  $p =$   
583  $0.31$  for *V. spiralis* high-density).

584



585  
586

587 **Figure 8.** Relationship between normalized depth-averaged velocity ( $u_{\text{mean}}/U_0$ ) and drag forces per plant  
 588 total surface area ( $\text{N m}^{-2}$ ) downstream of vegetation canopies. Different coloured symbols (blue–green–  
 589 yellow gradient) indicate the position of the measurement point ( $x$ ) normalized by the patch length  $L$  (60  
 590 cm for all configurations). Solid (dashed) lines correspond to significant (non-significant) Pearson’s  
 591 correlation.

## 592 4 Discussion

593 Vegetation canopies influence flow, sedimentation patterns and ecological processes in shallow  
 594 aquatic ecosystems. While some factors that influence the sheltering effect behind vegetation  
 595 patches have been investigated using vegetation mimics, this study is one of the first to compare  
 596 different species of live macrophytes. We found that  $L_{w1}$  was longer behind channel-spanning  
 597 patches than for finite-width patches, as expected given the increase in patch size, and extended  
 598 to equal or more than 2.5 patch lengths (from the patch leading edge) for all species. For the  
 599 finite-width patches, the steady wake length  $L_{w2}$  was also found to be related to the smallest  
 600 dimension between the canopy half-width ( $W/2$ ) and height ( $h$ ). When normalized by the  
 601 smallest of these patch dimensions, the steady wake length was comparable within each species,  
 602 except for *C. platycarpa* and *V. spiralis* (low density) in the channel-spanning configuration. A  
 603 second result of this study is that the velocity profiles downstream of channel-spanning real  
 604 vegetation were vertically non-uniform, exhibiting a two-layer pattern that was absent behind  
 605 finite-width patches, where it was compensated by a flow acceleration on the sides (Figure 9).  
 606 Therefore, a shift from channel-spanning to finite-width vegetation appears to induce different  
 607 flow patterns (vertical versus longitudinal variation in the flow velocity profiles), while differing  
 608 patch properties (plant species and density) influence the magnitude of the process (the length of  
 609 the steady wake region).

### 610 4.1 Steady wake length behind live macrophyte species: role of morphological 611 characteristics and biomechanical traits

612 The results of this study indicate that patches of *G. densa* produced the longest wake regions for  
 613 both  $L_{w1}$  and  $L_{w2}$  in the finite-width cases among the three species. This result might be explained  
 614 by this species' more rigid stems, whose flexural stiffness was an order of magnitude higher than  
 615 that of *C. platycarpa* and *V. spiralis* (Table 1). This result can also be partly attributed to  
 616 morphological characteristics because patches of *G. densa* were the sparsest in terms of biomass  
 617 and frontal area per canopy volume. When considering patches of finite width, *C. platycarpa* and  
 618 *V. spiralis* (at both high and low densities) produced identical wake lengths. The former had a  
 619 higher density and biomass per surface area, and was also the most flexible species among the  
 620 studied plants; thus, a shorter wake would be expected based on previous studies (Chen et al.,  
 621 2012; Zong & Nepf, 2012; Liu et al., 2021). The wake lengths were identical despite their  
 622 different morphologies: *C. platycarpa* has thin, highly branched stems, while *V. spiralis* is a  
 623 rosette species with strap-like leaves. Regardless, both exhibit streamlined morphologies that are  
 624 adapted to running-water environments. We also observed that the finite-width patches of these  
 625 two species adjusted their shape so that an increase in width was buffered with a decrease in  
 626 patch height, which resulted in a small difference in channel blockage between the two finite-  
 627 width cases and could explain the small difference in steady wake lengths. *Callitriche stagnalis*,  
 628 a morphologically similar species, exhibits a decrease in drag coefficient with flow velocity due  
 629 to reconfiguration of its shape (Siniscalchi & Nikora, 2012). Across channel-spanning cases, *C.*  
 630 *platycarpa* had the longest wake region  $L_{w2}$  of all three species. This indicates that the trends in

631 steady wake length  $L_{w2}$  with increasing patch size were not consistent across species. The co-  
632 variation of patch characteristics could explain the contrasting patterns. For *C. platycarpa*, entire  
633 patches directly sampled in the field were used and their density changed with patch size: smaller  
634 patches, at the start of their growth, were sparser. The other two species showed decreasing  
635 density with patch size, which is likely an experimental artifact due to the difficulty of keeping a  
636 constant spacing between plants of variable height, shoot biomass, number of leaves and  
637 branches across patch sizes. The strong co-variation between patch characteristics, as the one  
638 observed between patch density and size for *C. platycarpa*, suggests that not all combinations of  
639 patch characteristics might occur in nature and shows the need for more studies on real  
640 vegetation and real patches.

641 Similar findings with regard to the importance of the minimum patch dimension (width  
642 or height) in controlling wake length for submerged vegetation were found in Hu et al. (2018),  
643 where the impact of flexible leaf mimics on the flow structure was considered. The steady wake  
644 lengths for flexible cases are longer than those in this study ( $L_{xz}/\min(W/2, h) = 11.7\text{--}18.3$  for  
645 channel-spanning patches of width  $W = 40$  cm, where  $L_{xz}$  is the distance from the patch edge to  
646 the recirculating eddy;  $L_{xy}/\min(W/2, h) = 2.4\text{--}3.8$  for finite-width patches of width  $W = 10$  cm,  
647 where  $L_{xy}$  is the distance from the patch edge to the onset of the von Karman vortices). The  
648 degree of submergence fundamentally controls wake flow dynamics (Ortiz et al., 2013; Elliott et  
649 al., 2019). Marjoribanks et al. (2019) found that the wake length downstream of flexible  
650 saltmarsh vegetation was determined by patch height rather than patch width. However, we  
651 found that both patch dimensions could determine wake length, depending on their relative size  
652 (consistent with the findings in Hu et al. 2018). We also considered fully submerged patches,  
653 while salt marsh vegetation can either emerge or be submerged depending on the tidal cycle.  
654 Finally, the plants in Marjoribanks et al. (2019) were more rigid, with a flexural stiffness that  
655 varied on the order of  $10^{-5}$  to  $10^{-3}$  N m<sup>2</sup>, while in the proposed study, it varied between  $10^{-5}$  and  
656  $10^{-6}$  N m<sup>2</sup> (Table 1).

657 The effect of patch shoot density on wake length was dependent on patch configuration.  
658 For finite-width patches of *V. spiralis*, wake lengths were constant despite reducing the shoot  
659 density by half. However, decreasing shoot density increased the wake length in the channel-  
660 spanning case. This effect of shoot density agrees with the findings of Chen et al. (2012) and  
661 Zong & Nepf (2012), who explained this phenomenon as greater flow through the low-density  
662 patch displaces the vortices further downstream. We caution that the effect of shoot density was  
663 tested on a single species and that the density reduction may not have been sufficient to induce  
664 significant differences in flow structure. Because we focused on patches, the density could not be  
665 too low (cf. definition of patch in Schoelynck et al. (2018)). Low shoot densities would  
666 constitute a bed of sparse plants, which is also a relevant and related question. Future research  
667 should test a broader range of patch densities to quantify the effects on downstream flow  
668 structure.

#### 4.2 Sheltering and drag reduction in the wake of macrophyte patches

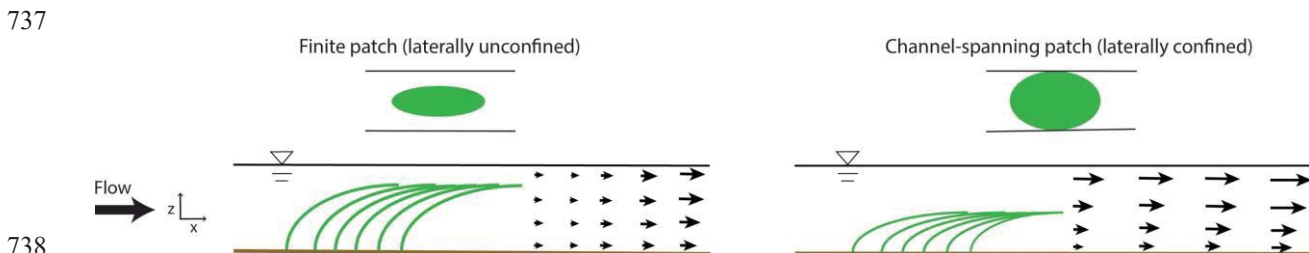
669  
670 A key difference in downstream flow patterns was observed in the two contrasting spatial  
671 configurations of vegetation. For channel-spanning patches, near-bed flow attenuation prevailed  
672 for longer distances. For finite-width patches, flow was attenuated throughout the water column,  
673 possibly facilitating larger organisms, such as macrophytes. This result is supported by the  
674 measurement of drag forces on plants at different distances downstream of the canopy, where  
675 drag force reduction for all species was significantly related to downstream flow modifications  
676 for cases where  $W < h$ . In these cases, only a few measurement points fell inside the sheltered  
677 wake region or at a distance  $< 2 L_{w2}$ , and drag forces increased as the velocity recovers up to the  
678 original value upstream of the patch. Instead, we found no significant correlation between drag  
679 forces and downstream flow modifications behind channel-spanning patches. Compared to the  
680 finite-width patches, most points fell within a distance that is less than two times the wake  
681 length. One metre downstream of the patch, the velocity was still lower than the incoming flow  
682 speed, and therefore, all points fell in a rather limited range of velocities (except in the case of *G.*  
683 *densa*), which could explain the lack of correlation. While this study identified trends in drag  
684 force with increasing velocity, these trends must be confirmed in future research due to the level  
685 of uncertainty compared to the variation in drag forces. Therefore, we can conclude that drag  
686 reduction behind patches might be significant in certain conditions and thus participate in the  
687 recruitment and protection of other organisms that are possibly less tolerant to flow stress. These  
688 results also confirm that vegetation patches are an important factor of flow heterogeneity in  
689 rivers and contribute to habitat construction.

#### 4.3 Ecological implications of downstream flow patterns in field conditions

690  
691 This study provides a basis to transfer the theory and results from fluid mechanics studies to  
692 understand flow patterns around real vegetation in natural conditions. The modification of  
693 hydrodynamic forces and the rates of sediment deposition vary depending on the vegetation  
694 characteristics, such as species morphological characteristics and biomechanical traits or canopy  
695 architecture (Sand-Jensen & Mebus, 1996; Sand-Jensen, 1998; Marjoribanks et al., 2019).  
696 Regardless, this study identifies appropriate scaling parameters that relate the length over which  
697 we observe flow attenuation to vegetation properties that are easily measurable in the field  
698 (canopy width and height). For example, the patch width to canopy height ratio in *C. platycarpa*  
699 has been reported to be  $2.5 \pm 1.3$  in Licci et al. (2019) and 1.6 in Sand-Jensen and Pedersen  
700 (2008), suggesting that the steady wake length  $L_{w2}$  will scale with the canopy height. Similarly,  
701 for *G. densa*, patches can be up to a few metres in width, while plant shoots are generally 0.2 m  
702 high (Cornacchia et al., 2018), which also suggests that patch wakes behind this species are  
703 influenced by canopy height. Given the consistency across the two definitions of steady wake  
704 length, similar considerations can be made for  $L_{w1}$ . However, care should be taken when  
705 extending the results of this study into field conditions because the experimental flume was  
706 narrower and more constrained than typical natural streams.

707 Considering the dimensional values of the steady wake length  $L_{w2}$ , this area of reduced  
 708 velocity ranges from 0.05–0.15 m behind the narrowest (finite-width) patches, and is much  
 709 longer (0.40–0.70 m) for the widest (channel-spanning) patches. The steady wake represents a  
 710 rather large, sheltered zone in the middle of a running-water environment, which plays a  
 711 significant role in habitat creation, growth and establishment of other organisms. As mentioned  
 712 above, relatively small patches of 60 cm in length were used in the experiments. Patches are  
 713 known to grow much longer in natural streams (e.g., Licci et al. (2019) investigated *C.*  
 714 *platycarpa* canopies up to 2.5–3.0 m long). We can thus expect patch length to play a role in the  
 715 sheltering effect, in relation to the interior adjustment length and the shear layer growth length  
 716 (Rominger & Nepf, 2011). Therefore, we could also expect much longer steady wake zones for  
 717 longer patches in field conditions.

718 In addition, the results of this study emphasize the importance of choosing realistic patch  
 719 dimensions (height, width and their ratio) when building artificial patches for studies in fluid  
 720 mechanics. Many additional factors create complexity when conducting experiments with real  
 721 vegetation. Plant reconfiguration changes with buoyancy, which is in turn affected by  
 722 photosynthesis and light; thus, the position of a given plant at a particular time could vary within  
 723 the same day. Flexural stiffness changes with position along the stem as well as with plant age  
 724 (young versus old patches). Thus, while mimics have constant and stable properties over time,  
 725 live vegetation displays changes on different timescales. Finally, future research should  
 726 investigate the relationship between wake length and the spacing between vegetation patches  
 727 observed under natural conditions. Aquatic plants grow in regularly spaced patterns oriented  
 728 parallel to the main flow direction (Cornacchia et al., 2018). The region of sheltered velocity  
 729 behind a patch may have an effect on the regularity of the pattern. Gap sizes are commonly  
 730 approximately 1.0 m (L. Cornacchia, personal observation), which is higher than the wake length  
 731 in this study and could be due to this study using smaller patches than average. Thus, the steady  
 732 wake length may determine the spacing between vegetation patches. This aspect is yet unknown  
 733 and deserves further investigation. Because vegetation modifies hydrodynamic conditions and  
 734 captures suspended sediment particles, a better understanding of the effects of vegetation on  
 735 water flows and sediment deposition is needed to predict the future development of aquatic  
 736 landscapes.



739 **Figure 9.** Schematic representation of the flow patterns downstream of finite (unconfined) and channel-  
 740 spanning (confined) patches. Velocity profiles downstream of channel-spanning vegetation are vertically

741 non-uniform, exhibiting a two-layer pattern, which is absent for finite-width patches and is compensated  
742 by a flow acceleration on the sides.

743

## 744 **5 Conclusions**

745 This study investigated the flow patterns, steady wake length and the drag force on a plant  
746 behind flexible submerged vegetation patches in an outdoor flume setting. The goal of this study  
747 was to test the effect of the patch aspect ratio, species differences and shoot density on the steady  
748 wake length behind patches of live vegetation, in contrast to previous studies that used plant  
749 mimics. The primary conclusions of this study are:

- 750 1. The results of this study provide new evidence that two fundamental patch dimensions,  
751 namely canopy half-width and height, appear to be important factors that determine the  
752 steady wake length. Channel-spanning patches generally produce a longer steady wake  
753 region than finite-width patches, according to both definitions of wake (based on the  
754  $0.5U_0$  velocity limit or as the distance until flow reaccelerates). However, we also  
755 highlight that patterns of hydrodynamic sheltering behind live patches can be complex  
756 and difficult to predict based only on patch dimensions due to the co-variation between  
757 different patch characteristics (such as density and patch size), pointing to the difficulty  
758 to separate the effect of different properties when using real vegetation.
- 759 2. This study is one of the first to confirm for live vegetation that a shift from channel-  
760 spanning patches to those with finite lateral extent yields a change in hydrodynamic  
761 processes (vertical vs. longitudinal inhomogeneities in the flow velocity profiles), while  
762 differing patch properties (plant species and density) influence the magnitude of the  
763 process (the length of the steady wake region). The dimensional values of the steady  
764 wake length  $L_{w2}$  range from 0.05 to 0.70 m, which represents a rather large, sheltered  
765 zone of reduced drag and flow velocity that plays a significant role in habitat creation,  
766 recruitment and protection of other organisms.

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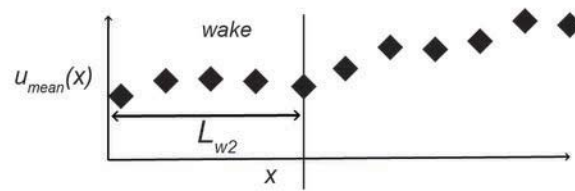
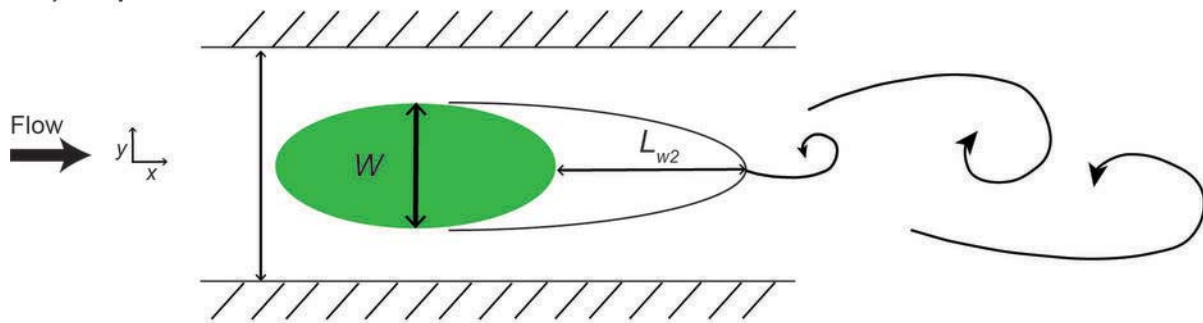
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- 976
- 977

Figure 1.

A) Top view



B) Side view

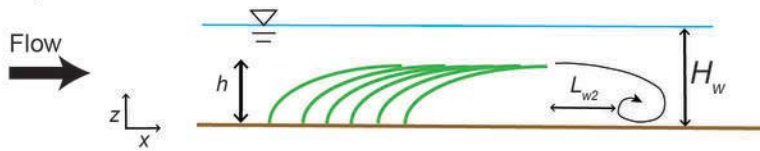


Figure 2.



*G. densa*

*C. platycarpa*

*V. spiralis*

A)



B)

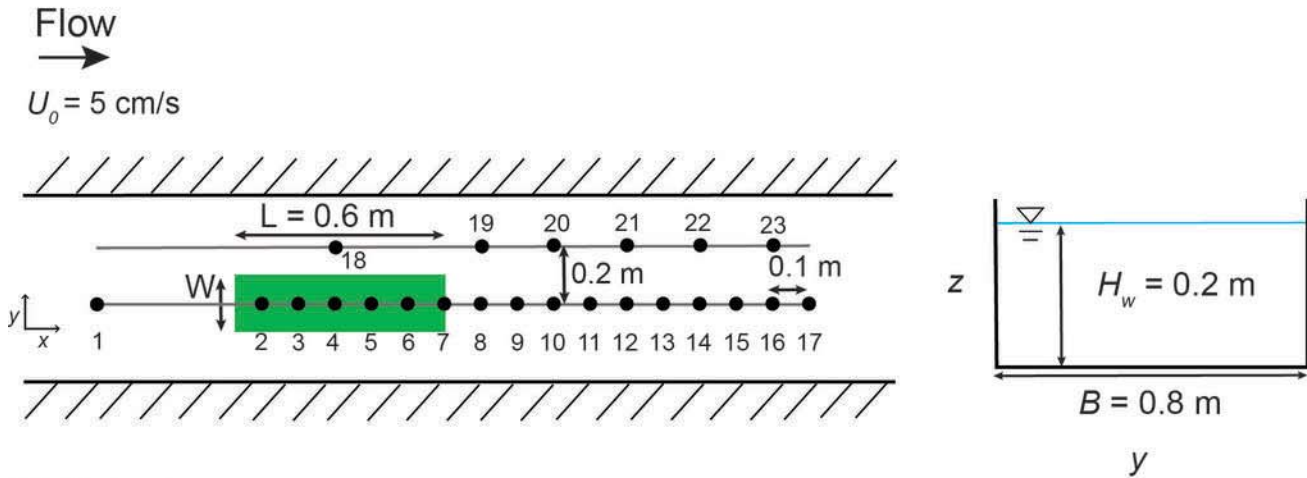


C)



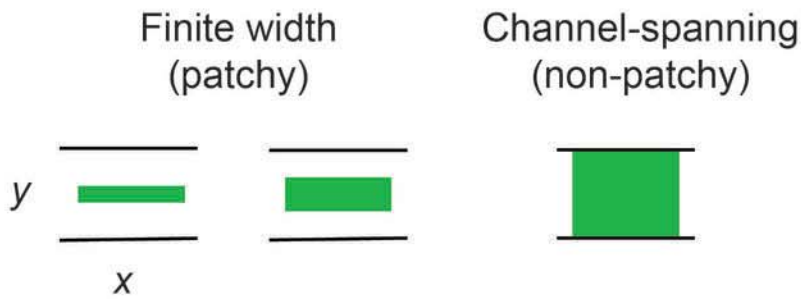
Figure 3.

## A) ADV profile measurements

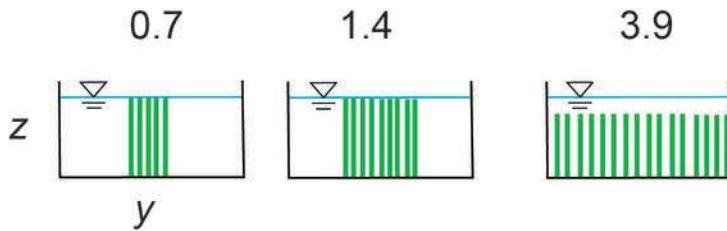


## B) Cases

### 1. Spatial configuration

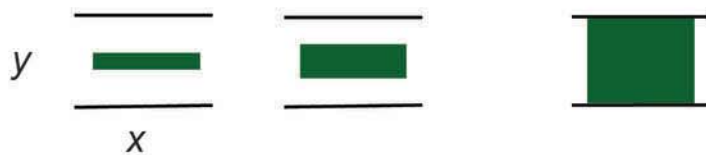


### 2. Patch aspect ratio (width/height)



### 3. Density

High density: 567 shoots/m<sup>2</sup>

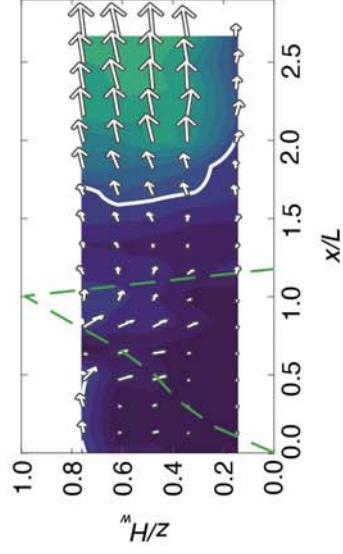


Low density: 310 shoots/m<sup>2</sup>



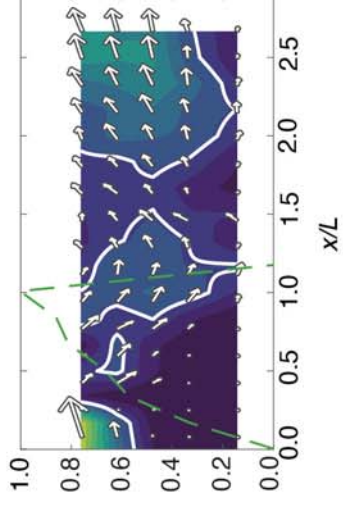
Figure 4.

Finite-width patch  
 $W/h = 0.7$



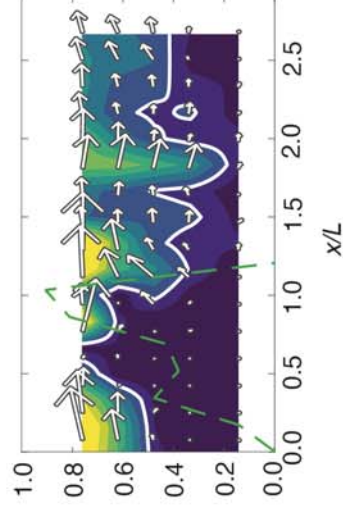
*Vallisneria spiralis* (Low density)

Finite-width patch  
 $W/h = 1.4$



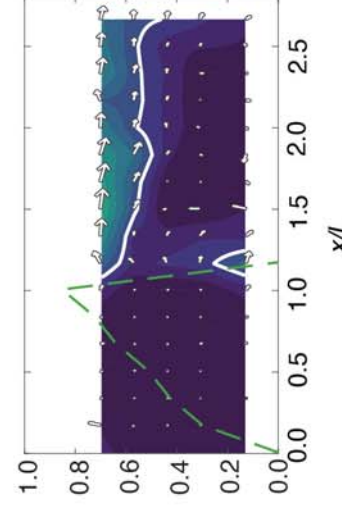
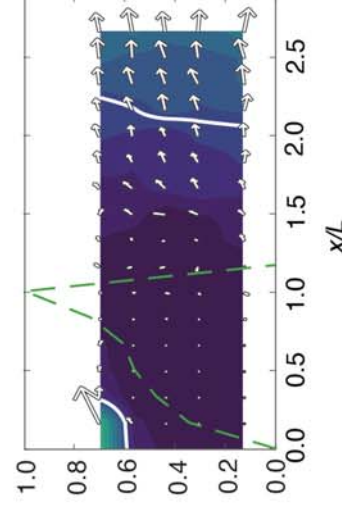
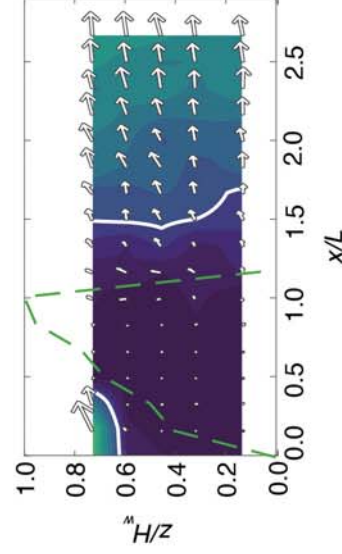
*Callitriche platycarpa*

Channel-spanning patch  
 $W/h = 3.9$

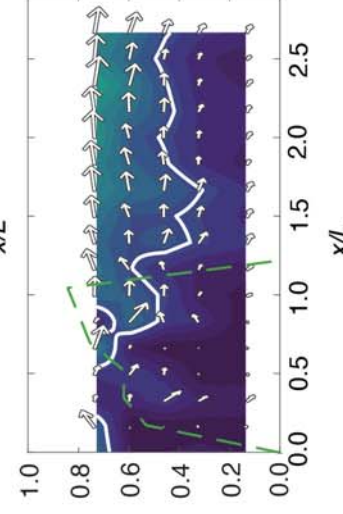
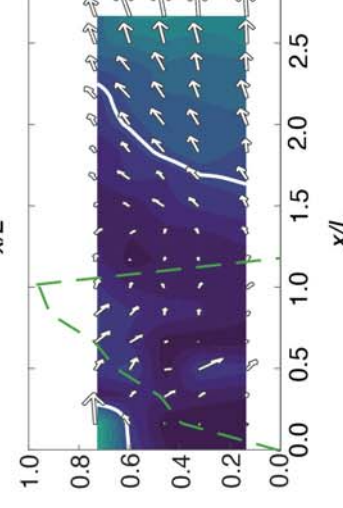
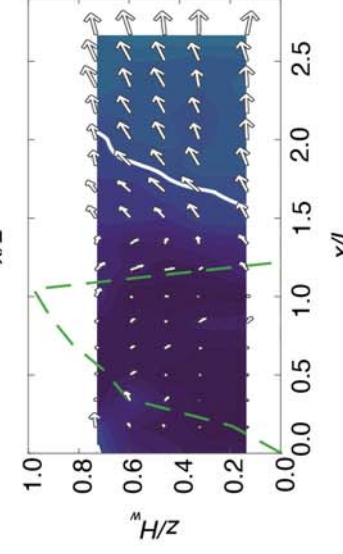


*Groenlandia densa*

*Vallisneria spiralis* (High density)



*Vallisneria spiralis* (High density)



*Vallisneria spiralis* (Low density)

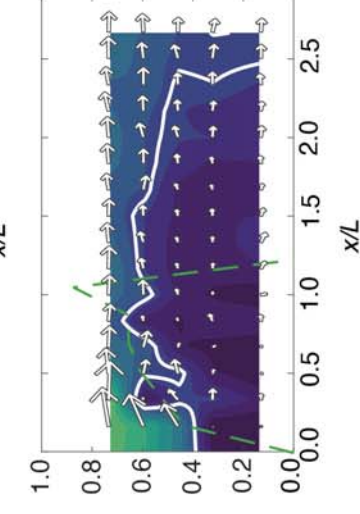
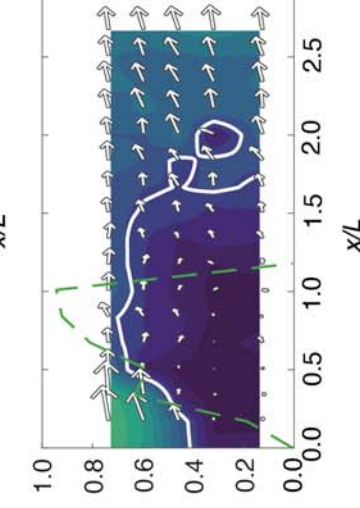
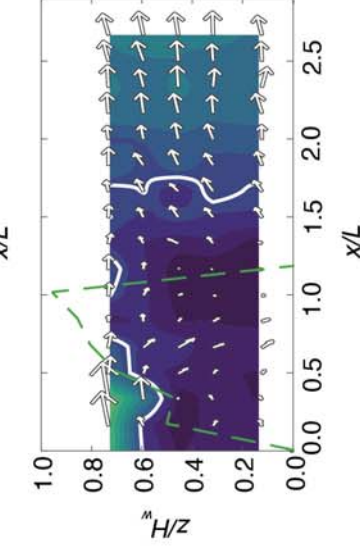
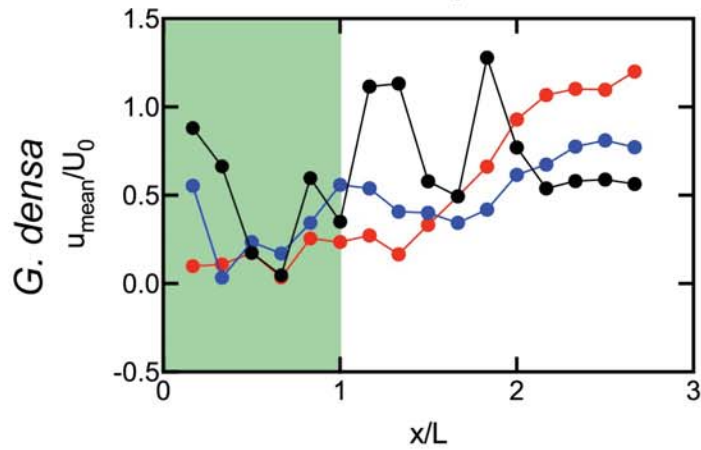
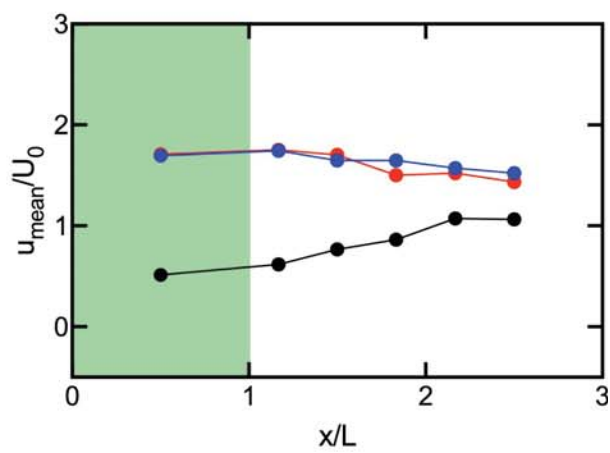
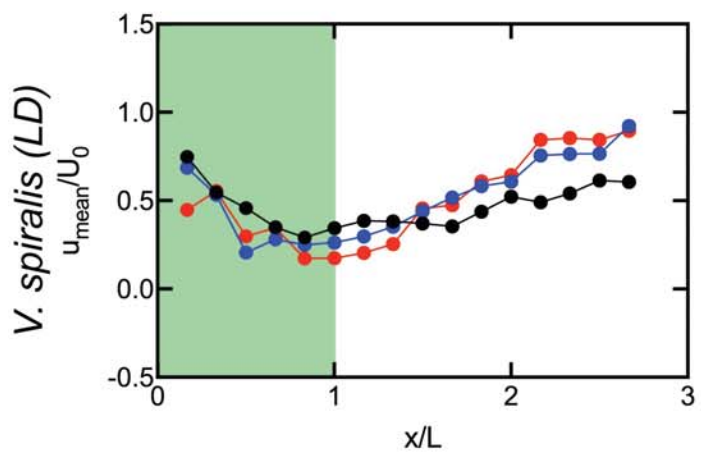
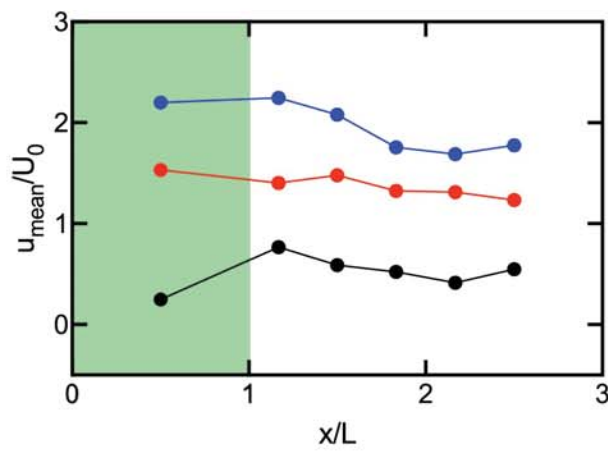
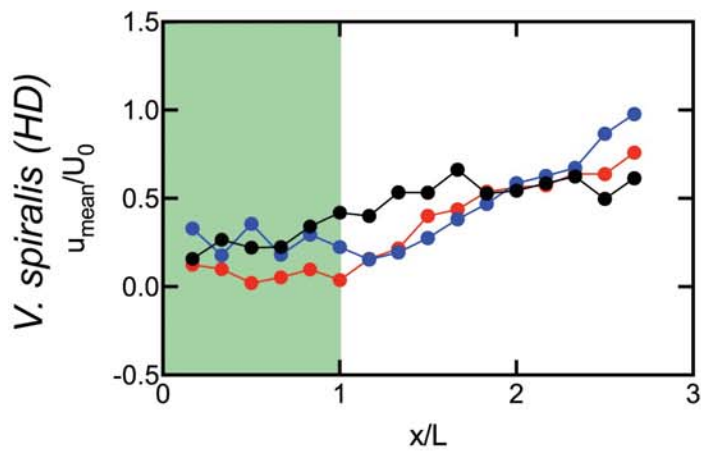
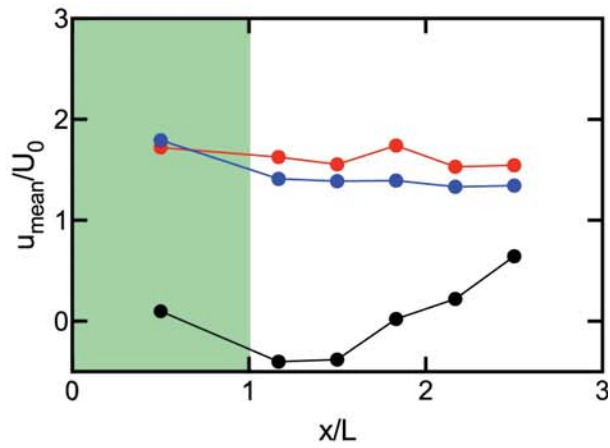
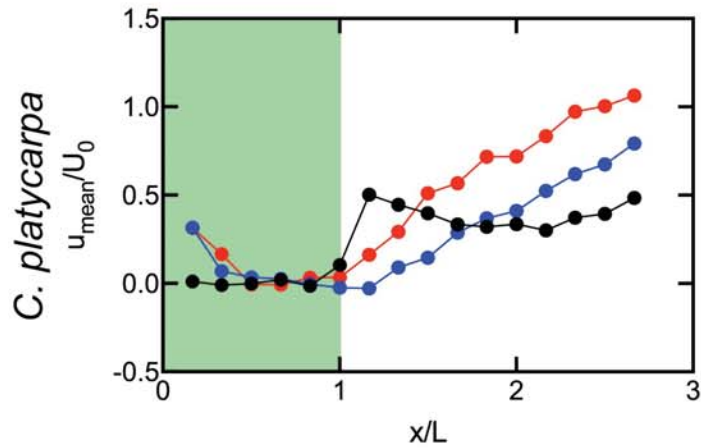
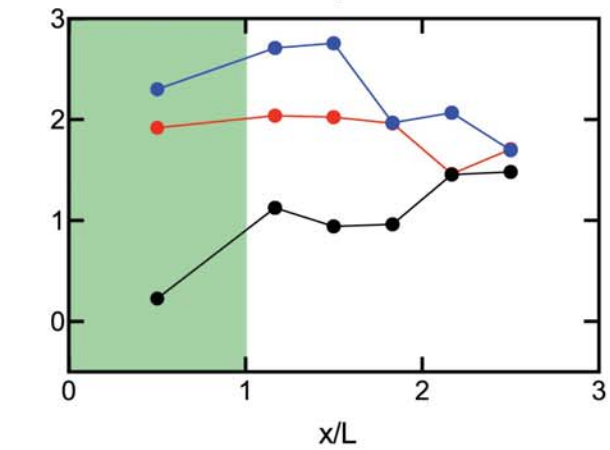


Figure 5.

Centerline profiles



Lateral profiles



Canopy aspect ratio ( $W/h$ ): ● 0.7

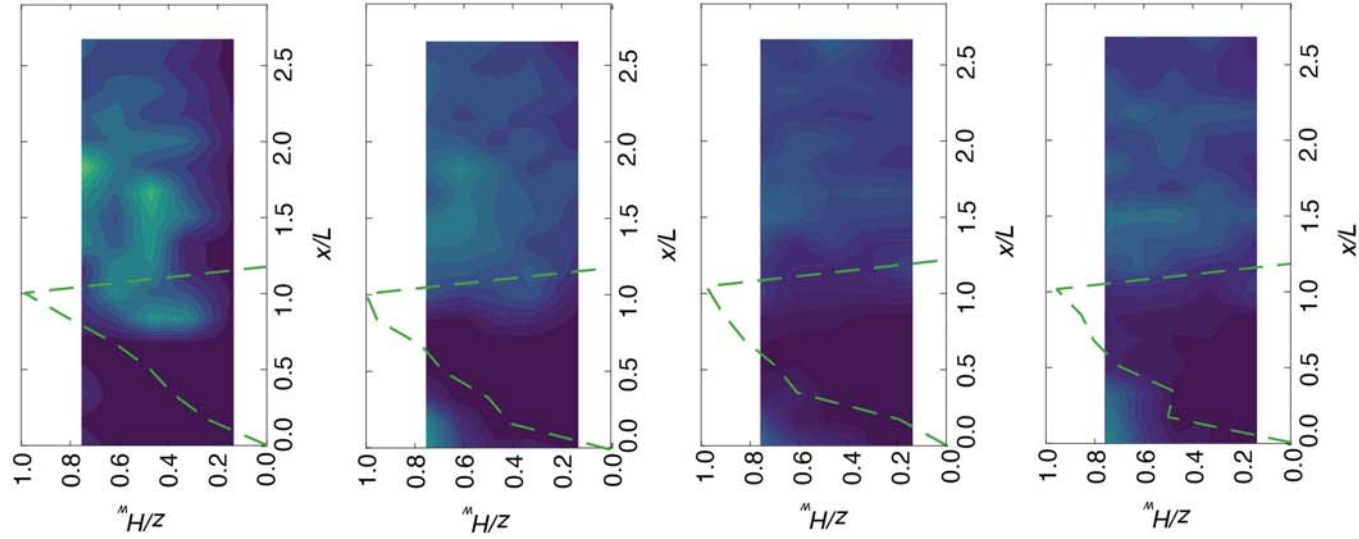
● 1.4

● 3.9

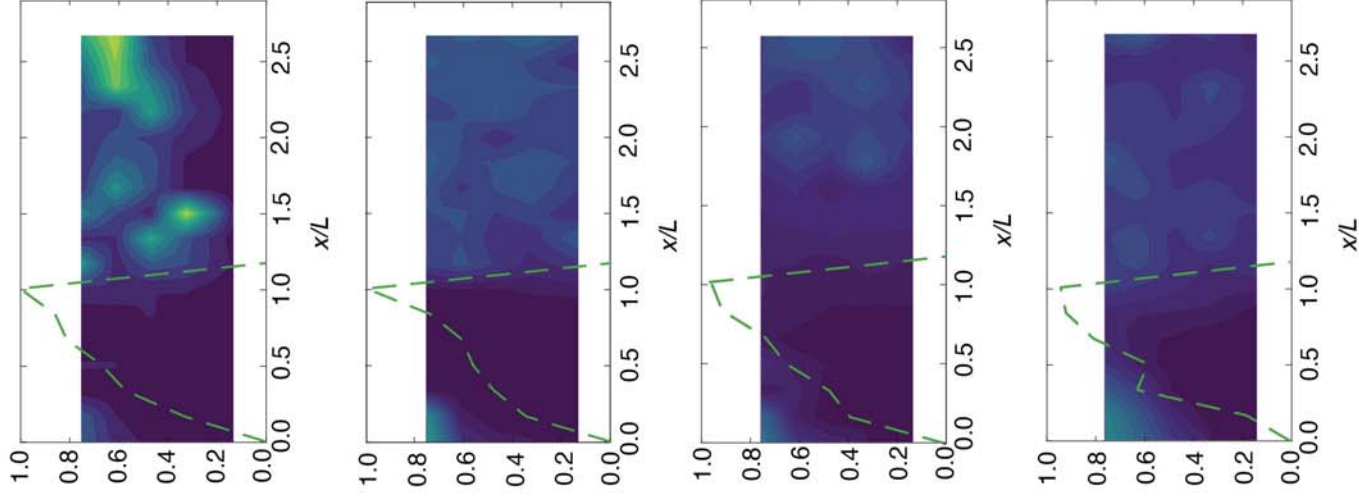
Figure 6.



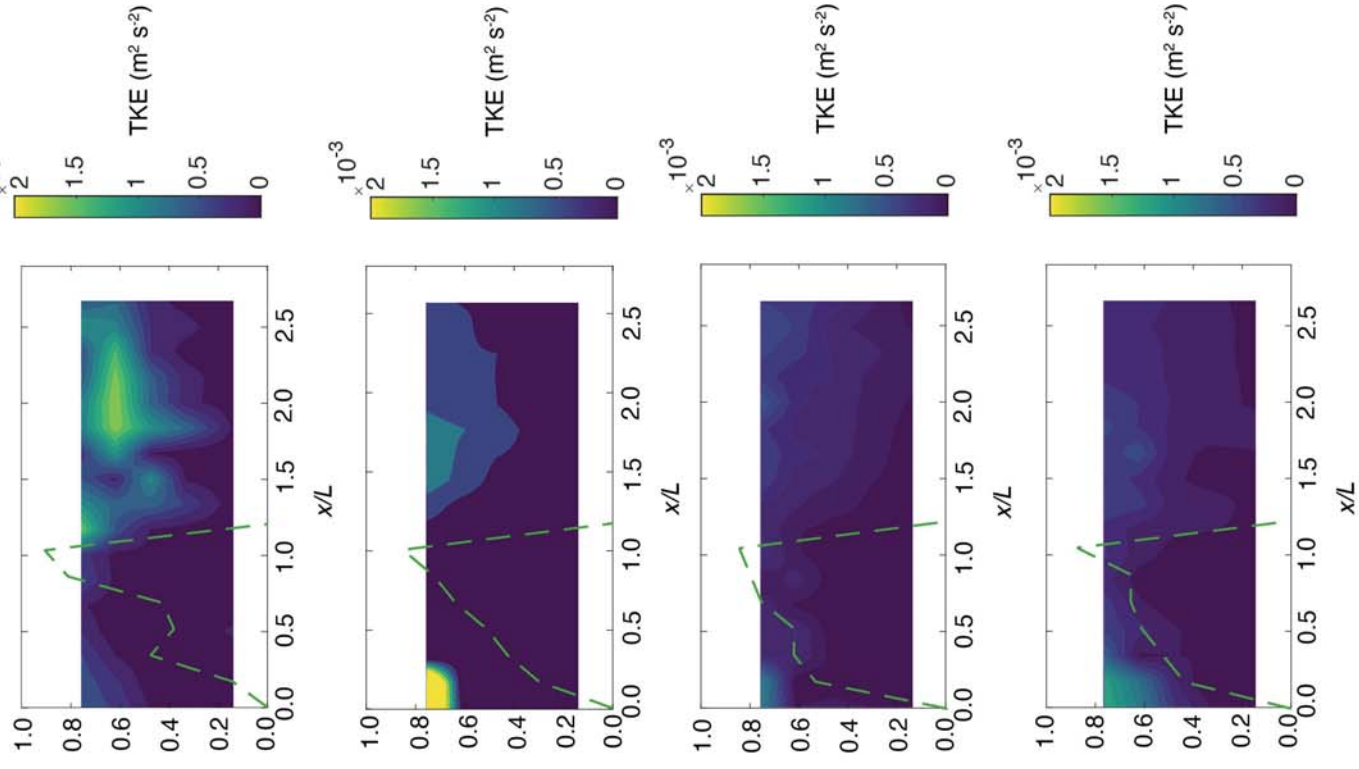
Finite-width patch  
 $W/h = 0.7$



Finite-width patch  
 $W/h = 1.4$



Channel-spanning patch  
 $W/h = 3.9$



*Groenlandia densa*

*Callitriche platycarpa*

*Vallisneria spiralis*  
(High density)

*Vallisneria spiralis*  
(Low density)

Figure 7.

Finite -patch configurations

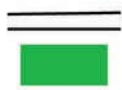
Channel-spanning configuration



W/h = 0.7



W/h = 1.4



W/h = 3.9

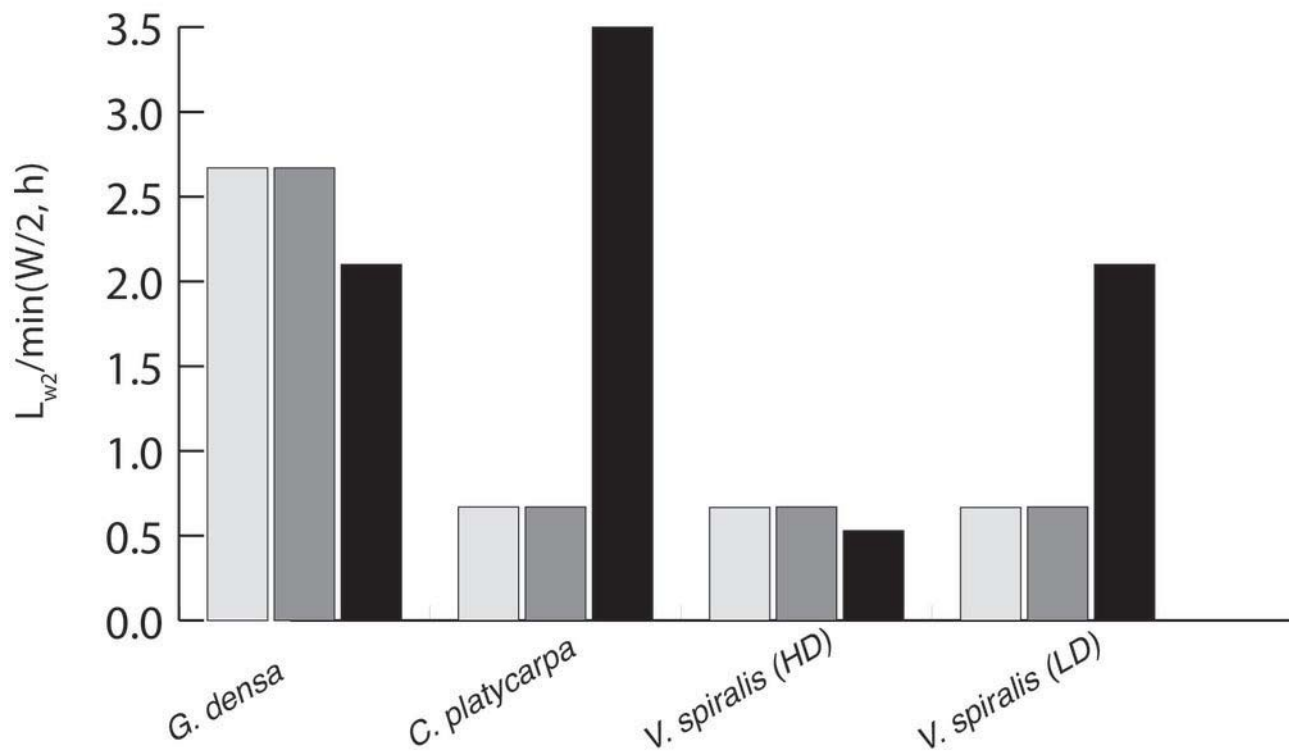


Figure 8.

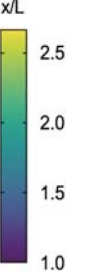
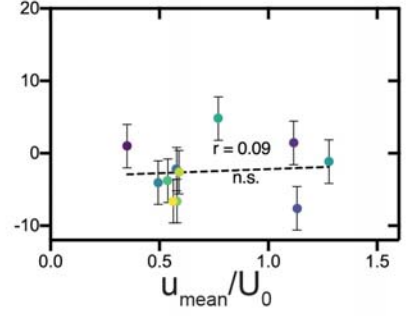
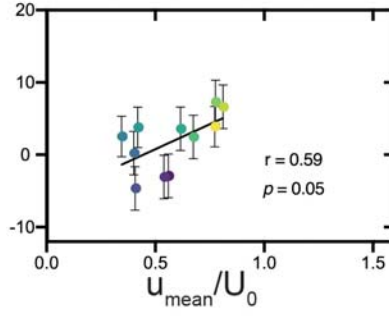
Canopy aspect ratio (W/h)

W/h = 0.7

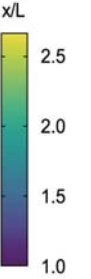
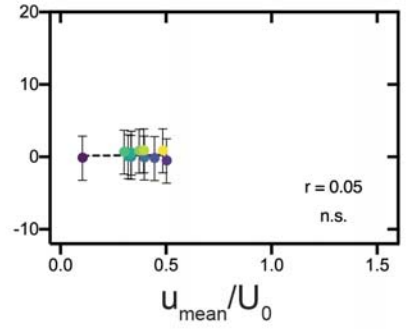
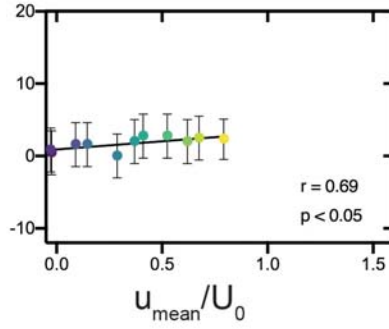
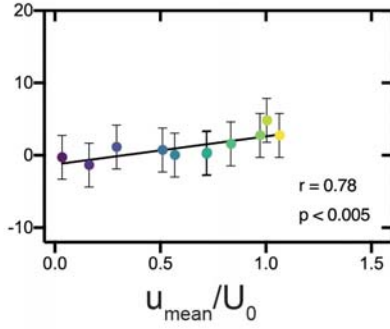
W/h = 1.4

W/h = 3.9

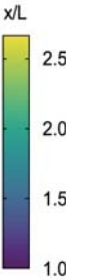
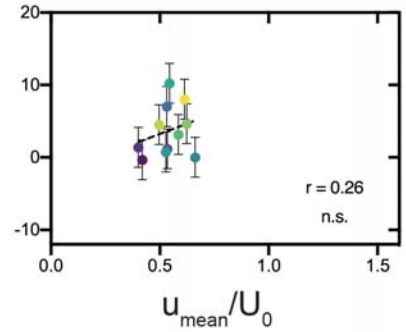
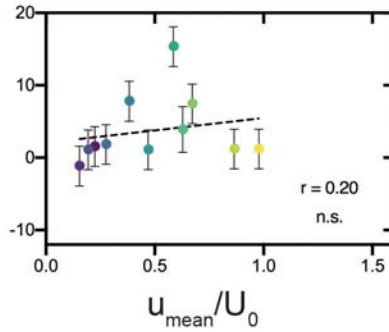
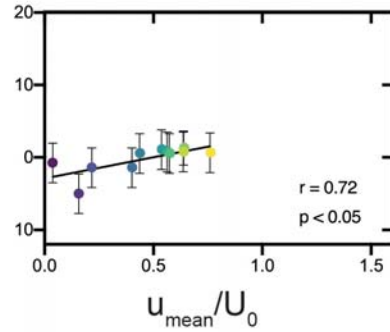
*G. densa*  
Drag force per total  
surface area (N m<sup>-2</sup>)



*C. platycarpa*  
Drag force per total  
surface area (N m<sup>-2</sup>)



*V. spiralis (HD)*  
Drag force per total  
surface area (N m<sup>-2</sup>)



*V. spiralis (LD)*  
Drag force per total  
surface area (N m<sup>-2</sup>)

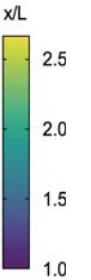
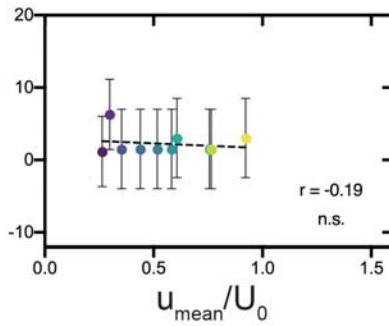
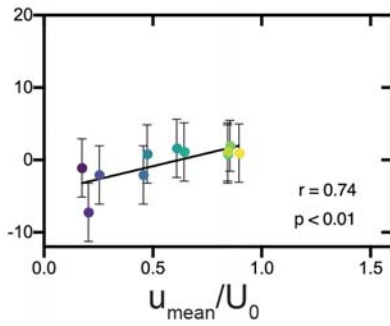
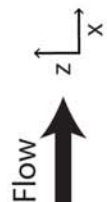
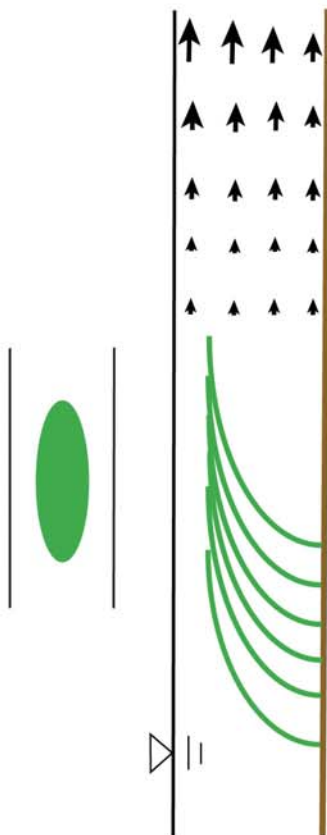


Figure 9.



Finite patch (laterally unconfined)



Channel-spanning patch (laterally confined)

