

# Flow and Wake Length Downstream of Live Submerged Vegetation Patches: How Do Different Species and Patch Configurations Create Sheltering in Stressful Habitats?

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

# Loreta Cornacchia<sup>1</sup>\*, Nicolas Riviere<sup>2</sup>, J. John Soundar Jerome<sup>2</sup>, Delphine Doppler<sup>2</sup>, Félix Vallier<sup>1</sup>, Sara Puijalon<sup>1</sup>

- <sup>1</sup> Univ Lyon, Université Claude Bernard Lyon 1, CNRS, ENTPE, UMR 5023 LEHNA, F 69622, 43 Boulevard du 11 Novembre 1918, F-69100, Villeurbanne, France.
- <sup>8</sup> <sup>2</sup> Univ Lyon, Université Claude Bernard Lyon I, Ecole Centrale de Lyon, INSA Lyon,
- 9 CNRS, LMFA, UMR 5509, 43 Boulevard du 11 Novembre 1918, F-69100, Villeurbanne,
- 10 France.
- 11
- 12 Corresponding author: Loreta Cornacchia (<u>loreta.cornacchia@nioz.nl</u>)
- 13 \* Current address: NIOZ Royal Netherlands Institute for Sea Research, Department of
- 14 Estuarine and Delta Systems, P.O. Box 140, 4400 AC Yerseke, The Netherlands

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#### 16 Key Points:

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

#### 23 Abstract

Vegetated canopies modify water conveyance and bed stabilization in aquatic ecosystems, 24 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 by vegetation patch configuration and characteristics. We measured the sheltering effect of 27 28 different species and patch configurations by comparing the length of the steady wake region, defined in this study as (1) the zone where streamwise velocity is diminished to more than 29 half of the incoming velocity  $(L_{wl})$ , and (2) the distance downstream of the patch where 30 velocity begins to increase  $(L_{w2})$ . Then, we measured the drag experienced by a plant at 31 different downstream locations as a measure of sheltering for plants growing in the steady 32 33 wake. We found that  $L_{wl}$  for channel-spanning cases was longer than for finite-width cases and extended to  $\geq 2.5$  patch lengths from the patch leading edge, while  $L_{w2}$  for finite-width 34 patches was related to the smallest dimension between canopy half-width and height. Species 35 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 predict based only on patch dimensions, especially due to co-variation between patch 41 42 characteristics in real vegetation.

#### 43 **1 Introduction**

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

In running water habitats, vegetation often grows in patches, which are relatively 53 well-defined areas that differ from their surroundings (Forman, 1995). Patches generally 54 55 consist of a single species at a relatively high density, and their spatial properties (e.g., length, width) are identified by sharp edges compared to surrounding bare areas (Schoelynck et al., 56 2018). Flow velocities are attenuated and sedimentation is enhanced within the patches 57 (Bouma et al., 2007; Schoelynck et al., 2012; Licci et al., 2019); turbulence can either be 58 reduced inside the patches and promote sediment deposition (Schulz et al., 2003; Hendriks et 59 al., 2008), or it can increase at the plant stem scale, leading to resuspension of sediments 60 (Tinoco & Coco, 2016). Flow velocity and turbulence are also reduced downstream of the 61 62 canopy, leading to increased fine sediment deposition (Sand-Jensen, 1998). Although sediment deposition is enhanced behind the vegetation, scour patterns tend to form around the 63 vegetation (Bouma et al., 2007; Chen et al., 2012a; Follett & Nepf, 2012; Yager & 64 Schmeeckle, 2013) and partly contribute to the deposition behind vegetation patches. This 65 flow velocity reduction creates a sheltered region downstream of the vegetation, which is 66 considered a major process for the functioning of running water ecosystems (Cornacchia et 67 al., 2018; Baladrón et al., 2021). In physically harsh environments, a reduction in 68 environmental stress is important for the structure of natural communities (Bertness & 69 Callaway, 1994; Bruno et al., 2003). Running water habitats produce highly challenging 70 conditions (Denny, 1988; Vogel, 1994), with a continuous risk of mechanical failure, 71 dislodgement and downstream transport. Therefore, vegetation patches represent a major 72 shelter for several types of organisms. For example, macrophyte patches generate a protected 73 environment allowing the development of dense invertebrate communities (Gregg & Rose, 74 1985). Flow reduction by vegetation may also facilitate larger organisms (e.g. fish; Baladrón 75 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, 1924; Brooks et al., 2005; Carlson & Lauder, 2011). Vegetation can be considered a primary 78 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, 1998). 81

The presence of vegetation can partially reduce the stressful conditions of running water habitats in two primary ways. First, sheltering by vegetation can reduce drag forces (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 bed shear stress, an index of force per unit area on the bed that influences macroinvertebrates 86 living in this zone of velocity gradient (Statzner et al., 1988), and that has been related to 87 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 (Caffrey & Kemp, 1992), while a high bed shear stress can lead to fine sediment erosion and 90 91 poor nutrient availability. The influence of vegetation on these physical components of the habitat gives rise to a niche with low stress in a highly stressful environment, which can 92 93 increase biodiversity (Cornacchia et al., 2018).

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

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

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



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Figure 1. Schematic representation of the flow patterns behind a submerged vegetation patch with flexible stems. The development of vortical structures in the **a**) horizontal and **b**) vertical planes controls the wake length  $L_{w2}$  (distance downstream of the patch before the velocity along the patch centreline begins to increase) and depends on patch density (Zong & Nepf, 2012), as well as patch width (W) and height, defined in this study as the deflected vegetation height (h). Modified from Liu et al. (2018).

In this study, we focus on how the steady wake downstream of live macrophyte patches 172 depends on the lateral confinement of vegetation (channel-spanning vs. finite-width patches) 173 and plant characteristics, and on their consequences for drag force reduction behind the 174 patches (an ecologically relevant process and an integral measure of plant adaptation to the 175 flow; Siniscalchi and Nikora (2012)). Specifically, we test the hypothesis that, for a patch of 176 given size and shape, different macrophyte species generate different steady wake lengths 177 based on their morphological characteristics and biomechanical traits. Within each 178 configuration, we vary (1) the patch aspect ratio (W/h), (2) the macrophyte species, and (3) 179 180 the shoot density. Then, we assess the direct sheltering effect of these species by measuring the drag force on a plant located at different distances downstream of the patch. Although the 181 182 growth of a plant would be different under natural conditions, the objective of this study is to provide a realistic quantification of the drag forces experienced by plants that attempt to 183 184 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 and 10 m long; and has a bed slope of 0.5%. The channel empties into a small, downstream 189 190 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 between 15.9 and 20.7 °C and was on average 18.7 °C, as measured by the temperature 195 sensor embedded in the Vectrino II profiler (Section 2.5). The water exits via pipes into a 196 stilling basin that ends in a double (spanwise and vertical) convergence before entering the 197 channel. The total discharge and weir height are adjusted to set the water depth at  $H_w = 0.2$  m 198 and the upstream mean water velocity at  $U_0 = 0.05$  m s<sup>-1</sup>. The flow is then turbulent 199 (hydraulic diameter based Reynolds number  $Re_{Dh} = 2.7 \ 10^4$ , considering a kinematic viscosity 200 of water  $v = 10^{-6} \text{ m}^2 \text{ s}^{-1}$ ) and subcritical (Froude number Fr = 0.04). Associated stem 201 Reynolds numbers, according to the average stem diameters of the different plants, are in the 202 range 90–360. The estimate of the length  $L_{dv}$  required for the flow development, using the 203 204 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 attached on a perforated metal grid (0.75 m  $\times$  0.5 m length) that was directly placed in the 220 221 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 generation. A plant shoot consists of a stem and leaves, but the size of the stem and leaves 223 224 (relative to each other) differs between the growth forms (Figure 2). For caulescent species (G. densa and C. platycarpa), the stem is developed with long internodes. For rosette species 225 226 (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, and  $5.89 \pm 1.09$  cm for V. spiralis at low density (variability given as the mean  $\pm$  SD of n = 3228

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





Figure 2. (A) *G. densa*, *C. platycarpa* and *V. spiralis* patches in the flume experiments; (B) 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) m <sup>-2</sup> ); frontal area per canopy volume $(a, m^{-1})$ , density (n. shoots m <sup>-2</sup> ), Young's modulus E
242	(MPa), second moment of area I (m <sup>4</sup> ), flexural stiffness EI (N m <sup>2</sup> )]. 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.

	Patch mo	rphological	l characteristics	Plant bio				
Species	Biomass per unit surface area (kg FM m <sup>-2</sup> )	Frontal area per canopy volume ( <i>a</i> , m <sup>-1</sup> )	Average density (n. shoots m <sup>-2</sup> )	E (MPa)	<i>I</i> (m <sup>4</sup> )	EI (N m <sup>2</sup> )	Total plant surface area (m <sup>2</sup> )	
G. densa	$\begin{array}{c} 1.31 \pm \\ 0.43 \end{array}$	1.84± 0.41	$1033\pm231$	$\begin{array}{c} 42.05 \pm \\ 16.28 \end{array}$	$(5.25 \pm 1.95) \times 1$ $0^{-13}$	$(2.11 \pm 0.91) \times 1$ $0^{-5}$	$\begin{array}{c} 0.017 \pm \\ 0.002 \end{array}$	
C. platycarpa	$\begin{array}{c cccc} ty carpa & 2.14 \pm & 13.97 \pm \\ 1.07 & 6.77 & 118 \end{array}$		$11841 \pm 5733$	$\begin{array}{c} 16.36 \pm \\ 0.14 \end{array}$	$(1.03 \pm 0.58) \times 1 \ 0^{-13}$	$(1.70 \pm 1.23) \times 1$ $0^{-6}$	$0.011 \pm 0.007$	
V. spiralis (High density)	1.57 ± 0.59	4.14 ± 1.78	$567\pm244$	155.13 ±	$(7.35 \pm 4.82) \times 1$	$(6.51 \pm 2.56) \times 1$	0.014 ± 0.004	
V. spiralis (Low density)	0.65 ± 0.23	$\begin{array}{c} 2.27 \pm \\ 0.89 \end{array}$	$310 \pm 221$	137.41	$0^{-14}$	0-6		

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

Biomechanical traits were measured through bending tests on 10 replicate individuals per species using a universal testing machine (Instron 5942, Canton, MA, USA). Mechanical forces act on the stems of species with a caulescent growth form, such as *G. densa* and *C.*  *platycarpa*, while the forces concentrate on leaves for species with a rosette growth form, such as *V. spiralis* (Hamann & Puijalon, 2013). Therefore, bending tests were performed on the basal part of the main stem of *G. densa* and *C. platycarpa* and on a single leaf of *V. spiralis*. Because we are working on flexible vegetation, the bending Young's modulus and flexural stiffness were chosen because they are relevant for the reconfiguration properties of the plants (Table 1).

270 Three-point bending tests were performed on leaf samples of V. spiralis. This test consists of a force applied at a constant rate of 10 mm min<sup>-1</sup> at the midpoint of a sample 271 placed on two supports (Silinski et al., 2018) with a support span of 60 mm. Due to the high 272 flexibility of stems of G. densa and C. playcarpa, a three-point bending test could not be 273 performed on these species. The samples were tested as cantilever beams using a one-fixed 274 275 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 sample by lowering a probe at a constant rate of 10 mm  $min^{-1}$ . 277

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





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

As shown in Figure 3b and Table 2, we compared a channel-spanning patch and two 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 patch. Because of co-variation between different patch properties (i.e., density also changes 307 with patch size), there is an overlap in the range of densities in the high- and low-density 308 309 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 density could not be kept constant across all species primarily due to differences in biomass 311 per shoot, which would have led to unrealistic patch characteristics. Other characteristics 312 differ between species (e.g., biomechanical traits, morphology, biomass distribution along the 313 314 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. platycarpa, and 7–43 cm for V. spiralis (Table 2). Such a large range is expected for natural 318 patches due to the differences in plant size between the plants in the front and rear of the 319 patch. The patch height in this study is defined as the deflected vegetation height (h). 320 321 Sideview pictures of the patches could not be taken because there was no transparent opening on the side of the outdoor flume. Using only three species also prevented us from performing 322 323 quantitative analyses to compare plant deflection with the biomechanical traits. The channel blockage factor of the patch (i.e., the share of the channel cross-section occupied by the 324 patch) was measured for all cases using underwater photographs. This parameter is relevant 325 326 because the flow forced through the patch may increase with increasing channel blockage, affecting the wake length (Zong & Nepf, 2012). 327

328 2.5 Flow velocity and turbulence measurements

Flow velocity profiles were measured using an Acoustic Doppler Velocimeter (ADV), the Nortek Vectrino II profiler with a down-looking probe. The Vectrino II was used to measure the profile in 5 bins with a 3.5-cm sample length and cell size of 0.1 cm over 3 minutes at 100 Hz, to cover the depth from 0 cm from the bed to 16 cm; the top part of the flow could not be measured by the profiler due to the down-looking probe. To minimize the bed interference on the velocity measurements, only the cells located in the upper 1.5 cm were used in the 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 3a, 5 profiles were measured in the vegetation canopy (points 2–6, every 10 cm) along the 337 patch centreline, one profile (point 7) at the downstream edge and 10 profiles downstream of 338 the vegetation (points 8–17, every 10 cm). To minimize interference by vegetation structures 339 within the sampling volume of the ADV probe and in the space between the probe and the 340 341 sampling volume, the stems were moved aside, while the probe started at the lowest measuring point for each vertical profile within the vegetation. This process prevented the 342 343 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 continuous movement of the plants with the current, leading to a measurement uncertainty of 346

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

Lateral profiles were measured along a line located 20 cm to the side of the patch centreline, and 20 cm from the flume wall. Along this line, one profile was measured halfway along the canopy length L (point 18 in Figure 3a), and 5 profiles were measured downstream of the canopy (every 20 cm; points 19–23 in Figure 3a). The velocity increase (in percent) at the lateral side of the patch was calculated as the difference between the depth-averaged velocity in profile 18 (located 20 cm to the side of the patch centreline) and the incoming 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 reliable data points, low-quality data points (i.e., correlation below the standard quality 360 threshold of 70% and signal-to-noise ratio (SNR) below 15 dB) were removed during 361 362 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, were separated into time averages  $(\overline{U}, \overline{V}, \overline{W})$ , and instantaneous turbulent fluctuations 365 (u'(t), v'(t), w'(t)) (e.g. as  $u'(t) = u(t) - \overline{U}$ , and similarly for v and w). The total turbulent 366

367 kinetic energy (TKE, m<sup>2</sup> s<sup>-2</sup>) was calculated as  $TKE = \frac{1}{2} \left( \overline{u'^2} + \overline{v'^2} + \overline{w'^2} \right)$ .

368 In this study, the steady wake length is characterized in two different ways. The first 369 definition,  $L_{wl}$ , indicates the most downstream distance (up to x/L = 2.6) where the streamwise velocity is diminished to more than half of the incoming velocity ( $u < 0.5U_0$ ), 370 371 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 velocity along the patch centreline begins to increase, as shown in Figure 1a, and denotes the 373 374 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 by turbulent structures from outside accelerates the flow in the wake, marking the end of the 376 zone sheltered by the canopy; however, defining the start of the velocity increase can be 377 378 difficult, especially with a limited number of measurements. Hence, we also considered  $L_{wl}$ 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 downstream velocity profile and was therefore set to 0.05 m. This estimation of the length of 382 383 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 et al., 2018). 387

388

#### 2.6 Drag force measurements

Drag forces were measured at points 7-17 (Figure 3a) using a custom-made force 389 390 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 direction with an uncertainty of  $\pm 0.05$  N. A base with a hole fitting the size of the transducer 392 393 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 the drag sensor (Bal et al., 2011). Similar considerations held for mounting the sensor on the 401 402 bed due to local irregularities and grain size. To compare between species, drag was expressed as a function of the total plant surface area (Table 1). Therefore, the total surface 403 area was obtained for each plant at the end of the drag measurements. The individual leaves 404 405 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 consistency (one set for G. densa, one set for C. platycarpa, one set for V. spiralis high-408

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

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

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

431

#### 3.2 Flow patterns around the reconfigured vegetation

Figure 4 shows the heights of the vegetation canopy along with plots of streamwise 432 433 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 and all cases, the canopy exhibited reconfiguration and particularly bending of the plants. 435 436 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 downstream plants (Barsu et al., 2016). Despite their bending, plants were sufficiently long to 438 still reach the water surface for finite-width cases  $(max(h/H_w) = 1)$ . This is consistent with 439 field conditions, where most species in shallow waters grow just below or on the water 440 surface: the submergence ratio  $h/H_w$  gradually increases with increasing patch length, 441 442 reaching values near 1 (Licci et al., 2019). Conversely, the plants remained below the water surface for channel-spanning cases  $(max(h/H_w) = 0.8-0.9, depending on the species)$ . The 443 444 channel blockage factor was similar between the two finite-width cases (Supporting Information Figure S1). The small difference in blockage factors between the two cases 445 results from adjustments of the patch where an increase in width was buffered with a 446 decrease in height; we observed less bending of the plants in the narrowest patch, except for 447 G. densa (cf. patch height and undeflected plant length in Table 2). 448

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 that of the incoming flow. However, due to the blockage effect in the channel-spanning case, 451 452 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 as the canopy reached the water surface  $(h/H_w = 1)$ , as shown in Figure 4 by the green dashed 456 line depicting the patch shape. This phenomenon leads to differences in the vertical velocities 457 observed within the patch; nearly absent in the channel-spanning case, downwards velocities 458 459 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 canopy is marginally less dense. In the two finite patch cases, the velocity increased at the 461 462 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% for V. spiralis in the high-density case and 82% in the low-density case. Differences between 465 466 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 downstream of the vegetation, with faster flow in the upper part of the water column and 468 attenuated flow near the bed. This is consistent with a relatively low TKE in the wake (Figure 469 5), except in the upper part corresponding to the boundary between the wake and the upper 470 471 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 (Kitsikoudis et al., 2017). The streamwise velocity however increased with longitudinal 482 distance from the canopy edge. The highest levels of  $-\rho \overline{u'v'}$  Reynolds stresses were observed 483 (Supporting Information Figure S3), characterizing a momentum injected by eddies in the 484 485 wake from the lateral free flows, consistently with the separated shear layers observed on the sides of patches of cylinders by Chang and Constantinescu (2015). 486

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

channel-spanning case, while profiles are not strictly identical. The centreline depth-averaged 492 velocity increased more rapidly to recover U<sub>0</sub> for the narrowest patch, which is consistent 493 494 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 patch of V. spiralis, least for the widest non-spanning 496 at patch.

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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
 sample of 10 plants per case.

Case	Species	Patch width W (m)	Mean patch height (m) ± SD	Max. patch height h (m)	Undeflected plant length (m)	Patch aspect ratio (W/L)	Patch aspect ratio (W/h)	Water height H <sub>w</sub> (m)	Patch density (n. shoots m- <sup>2</sup> )	Solid volume fraction (\$)	Length of steady wake L <sub>w1</sub> (m)	Length of steady wake $L_{w2}$ (m)
GRO1	G. densa	0.15	$\begin{array}{c} 0.12 \pm \\ 0.06 \end{array}$	0.21	$0.26\pm0.12$	0.25	0.71	0.21	1267	0.003	0.60	0.20
GRO2	G. densa	0.30	$\begin{array}{c} 0.15 \pm \\ 0.05 \end{array}$	0.21	0.21 ± 0.11	0.50	1.43	0.21	1028	0.003	> 1.0	0.40
GRO3	G. densa	0.75	$\begin{array}{c} 0.11 \pm \\ 0.06 \end{array}$	0.19	$0.21\pm0.05$	1.25	3.95	0.21	804	0.002	> 1.0	0.40
CAL1	C. platycarpa	0.15	$\begin{array}{c} 0.16 \pm \\ 0.05 \end{array}$	0.22	$0.21\pm0.08$	0.25	0.68	0.22	8133	0.009	0.40	0.05
CAL2	C. platycarpa	0.30	$\begin{array}{c} 0.14 \pm \\ 0.05 \end{array}$	0.23	0.24 ± 0.12	0.50	1.30	0.23	8946	0.010	0.70	0.10
CAL3	C. platycarpa	0.75	$\begin{array}{c} 0.14 \pm \\ 0.05 \end{array}$	0.20	$0.25 \pm 0.08$	1.25	3.75	0.23	18445	0.021	> 1.0	0.70
VAL1	V. spiralis	0.15	$\begin{array}{c} 0.16 \pm \\ 0.07 \end{array}$	0.21	$0.26\pm0.10$	0.25	0.71	0.22	833	0.004	0.60	0.05
VAL2	V. spiralis	0.30	$\begin{array}{c} 0.16 \pm \\ 0.05 \end{array}$	0.21	$0.28\pm0.10$	0.50	1.43	0.22	511	0.003	0.70	0.10
VAL3	V. spiralis	0.75	$\begin{array}{c} 0.16 \pm \\ 0.03 \end{array}$	0.19	$0.28\pm0.09$	1.25	3.95	0.22	356	0.002	> 1.0	0.10
VAL4	V. spiralis	0.15	$\begin{array}{c} 0.14 \pm \\ 0.04 \end{array}$	0.21	$0.24\pm0.09$	0.25	0.71	0.22	444	0.002	0.40	0.05
VAL5	V. spiralis	0.30	$\begin{array}{c} 0.15 \pm \\ 0.06 \end{array}$	0.21	$0.28\pm0.10$	0.50	1.43	0.22	278	0.001	0.60	0.10
VAL6	V. spiralis	0.75	$\begin{array}{c} 0.14 \pm \\ 0.03 \end{array}$	0.19	$0.28\pm0.09$	1.25	3.95	0.22	209	0.001	0.90	0.40



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**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<sub>0</sub>. The longitudinal distance (x/L) is normalized by the patch length L (60 cm for all configurations).



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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 511 different patch *W/h* ratios were considered. Green dashed lines indicate the height of the vegetation canopy.





517 3.3 Steady wake length

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

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

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

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  $L_{wI}$  is generally longer, there is consistency across the two 556 definitions.



557

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

#### 5623.4 Drag force measurements

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

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

- 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).

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



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

#### 592 **4 Discussion**

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

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

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

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

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

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

669

4.2 Sheltering and drag reduction in the wake of macrophyte patches

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

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

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

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

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







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**

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

- 1. The results of this study provide new evidence that two fundamental patch dimensions, 750 namely canopy half-width and height, appear to be important factors that determine the 751 steady wake length. Channel-spanning patches generally produce a longer steady wake 752 region than finite-width patches, according to both definitions of wake (based on the 753  $0.5U_0$  velocity limit or as the distance until flow reaccelerates). However, we also 754 highlight that patterns of hydrodynamic sheltering behind live patches can be complex 755 and difficult to predict based only on patch dimensions due to the co-variation between 756 different patch characteristics (such as density and patch size), pointing to the difficulty 757 to separate the effect of different properties when using real vegetation. 758
- 2. This study is one of the first to confirm for live vegetation that a shift from channel-759 spanning patches to those with finite lateral extent yields a change in hydrodynamic 760 processes (vertical vs. longitudinal inhomogeneities in the flow velocity profiles), while 761 differing patch properties (plant species and density) influence the magnitude of the 762 process (the length of the steady wake region). The dimensional values of the steady 763 wake length  $L_{w2}$  range from 0.05 to 0.70 m, which represents a rather large, sheltered 764 zone of reduced drag and flow velocity that plays a significant role in habitat creation, 765 recruitment and protection of other organisms. 766
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- 777 Data presented in this manuscript are available at the 4TU.Research Data repository
- 778 (<u>https://figshare.com/s/811456a0ad40aed1b55f</u>).

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976

Figure 1.



Figure 2.

G. densa





# V. spiralis

















Figure 3.

## A) ADV profile measurements





3. Density

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



Figure 4.



Figure 5.



Figure 6.



Vallisneria spiralis

Vallisneria spiralis

Figure 7.



Figure 8.



Figure 9.

