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Effect of patch length on physical parameters and nutrient conditions



	<i>Short patch</i>	<i>Long patch</i>
Streamwise velocity (\bar{u})	=	-
Sediment grain size (ϕ)	=	-
Organic matter content	=	+
Orthophosphate and ammonium concentrations (PO_4^{3-} , NH_4^+)	=	+
Nitrate concentration (NO_3^-)	=	-
Nitrite concentration (NO_2^-)	=	=

Highlights

- The habitat modification by plants patches in rivers depends on patch length
- In-patch velocity and sediment grain size are reduced for increasing patch length
- Sediment organic matter, PO_4^{3-} and NH_4^+ concentrations increase with patch length

1 **Scale-dependent effects of vegetation on flow velocity and biogeochemical conditions in**
2 **aquatic systems**

3

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18

19 ***Abstract***

20 In rivers, scale-dependent feedbacks resulting from physical habitat modifications
21 control the lateral expansion of submerged plant patches, while the mechanisms that limit
22 patch expansion on a longitudinal dimension remain unknown. Our objective was to
23 investigate the effects of patch length on physical habitat modification (i.e., flow velocity,
24 sediment grain size distribution), the consequences for biogeochemical conditions (i.e.,
25 accumulation/depletion of nutrients, microbial respiration), and for individual plants (i.e.,

26 shoot length). We measured all of these parameters along natural patches of increasing length.
27 These measurements were performed at two sites that differed in mean flow velocity,
28 sediment grain size, and trophic level. The results showed a significant effect of patch length
29 on organic matter content and nutrient concentrations in interstitial water. For the shortest
30 patches sampled, all of these parameters had similar values to those measured at the upstream
31 control position. For longer patches, organic matter content and orthophosphate and
32 ammonium concentrations increased within the patch compared to the upstream bare
33 sediment, whereas nitrate concentrations decreased, suggesting changes in vertical water
34 exchanges and an increase in anaerobic microbial activities. Furthermore, plant height was
35 related to patch length by a quadratic pattern, probably due reduced hydrodynamic stress
36 occurring for increasing patch length, combined with conditions that are less favourable for
37 plants over a threshold length, possibly due to the light limitation or to the high concentration
38 of ammonium that in the concentration range we measured may be toxic for plants. The
39 threshold lengths over which patches influence the nutrient concentrations were reduced for
40 the site with higher nutrient levels. We demonstrated that the plant-induced modifications of
41 the physical habitat exert important effects on biogeochemical conditions, with possible
42 consequences for patch dynamics and ecosystem functioning.

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44

45 **Keywords:** ecosystem engineering, plant patches, feedbacks, nutrient availability, sediment
46 characteristics, rivers.

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52 **1. Introduction**

53 Physical ecosystem engineers are organisms able to physically modify the abiotic
54 environment, inducing effects for other species or feedbacks for themselves (Jones et al.,
55 1994; 1997). The interaction between the ecosystem engineer and the environment may result
56 in net positive feedback (e.g., stress alleviation or increased availability of resources) or
57 negative feedback (e.g., stress aggravation or reduced availability of resources; Jones et al.,
58 1997; Hastings et al., 2007). When feedbacks are positive at short distances and negative at
59 long distances (i.e., scale-dependent feedbacks), engineering may lead to the formation of
60 regular patterns (or patchiness, Rietkerk and van de Koppel, 2008), as observed, for instance,
61 in bushy vegetation in arid ecosystems (Klausmeier, 1999; Barbier et al., 2006), tussock
62 vegetation in intertidal wetlands (van de Koppel and Crain, 2006), and, recently, submerged
63 aquatic vegetation in rivers (Schoelynck et al., 2012; Cornacchia et al., 2018). In streams,
64 submerged plants typically grow in patches (Fig. 1; Sand-Jensen and Madsen, 1992) and
65 affect ecosystem processes (Carpenter and Lodge, 1986) by modifying flows and sediment
66 dynamics (Wharton et al., 2006; Folkard, 2019). Patches are porous structures through which
67 flow can partially pass, but with a reduced velocity relative to the upstream conditions (Sand-
68 Jensen and Pedersen, 2008; Folkard, 2011; Vandenbruwaene et al., 2011; Nepf, 2012;
69 Marjoribanks et al., 2017; Licci et al., 2019), which causes the flow to deflect and accelerate
70 above and next to the canopy, locally increasing water velocity and turbulence at the edges of
71 the patch (Sand-Jensen and Mebus, 1996; Sand-Jensen and Pedersen, 2008; Sukhodolov and
72 Sukhodolova, 2010; Folkard, 2019). As a result, inside plant patches, the potential for
73 resuspension and erosion is reduced (Sand-Jensen, 1998; Schulz et al., 2003; Hendriks et al.,
74 2009), and fine sediment tends to accumulate compared to bare areas (Cotton et al., 2005;
75 Biggs et al., 2021), whereas flow acceleration next to the patch contributes to particle

76 entrainment and transport (Sand-Jensen, 1998; Schoelynck et al., 2013). As a consequence,
77 plant growth and thus patch expansion could be locally enhanced inside or immediately
78 downstream of a patch due to reduced hydrodynamic stress, a lower risk of mechanical
79 damage for plants (breakage, uprooting) and accumulation of fine particles (Wharton et al.,
80 2006; Jones et al., 2012; Biggs et al., 2021; Reitsema et al., 2021), which in turn increases
81 nitrogen and phosphorus concentrations (Sand-Jensen, 1998; Clarke and Wharton, 2001;
82 Sanders and Trimmer, 2006; Schoelynck et al., 2017) and enhances nutrient availability for
83 plants. Reciprocally, plant growth and thus patch expansion could be inhibited next to the
84 patch due to higher hydrodynamic stress and coarser sediment, leading to the formation of
85 regular patterns (Sand-Jensen, 1998; Schoelynck et al., 2012; Cornacchia et al., 2019).

86 Ecosystem engineering by aquatic plants also has important implications for
87 biogeochemical processes in rivers (Fig. S1, Gutiérrez and Jones, 2006; Trimmer et al., 2009;
88 Audet et al., 2021). In the case of submerged aquatic plants, the modification of flow and
89 sediment characteristics inside the patches (i.e., reduced flow and grain size) should lead to
90 reduced surface-subsurface water exchange (Findlay, 1995; Morrice et al., 1997), sediment
91 enrichment in organic matter and changes in nutrient concentrations (Dahm et al., 1987;
92 Sand-Jensen, 1998; Schulz et al., 2003; Cotton et al., 2005; Schoelynck et al., 2017). In
93 organic matter-rich sediment, ammonium concentrations increase through mineralization and
94 ammonification (Ladd and Jackson, 1982), and oxygen availability decreases, inducing
95 anaerobic microbial processes (Findlay, 1995; Morrice et al., 1997, Sanders et al., 2007).
96 Under anoxic conditions, denitrifying bacteria can transform nitrates into diatomic nitrogen,
97 reducing the nitrogen availability for the aquatic system (Verstraete and Focht, 1977;
98 Seitzinger, 1988, Gutiérrez and Jones, 2006). Ammonium is the main source of nitrogen for
99 aquatic plants, which is predominant in the interstitial water and assimilated by plant roots
100 (Barko and Smart, 1986; Barko et al., 1991). However, high concentrations of ammonium

101 resulting from high concentrations of sediment organic matter (Barko and Smart, 1983; Sand-
102 Jensen et al., 2005) can inhibit plant growth and photosynthesis (Rudolph and Voigt, 1986;
103 Britto and Kronzucker, 2002; Clarke and Baldwin, 2002; Nimptsch and Pflugmacher, 2007;
104 Cao et al., 2009; Su et al., 2012; Yu et al., 2015). This can induce oxidative stress (Cao et al.,
105 2004; Nimptsch and Pflugmacher, 2007; Cao et al., 2009), lead to internal carbon-nitrogen
106 imbalance (Cao et al., 2009) and even be toxic to plants. Therefore, aquatic plants may
107 influence microbial processes and nutrient availability, inducing positive or negative effects
108 on their own growth (Fig. S1).

109 The effects of aquatic plants on the physical habitat are dependent on patch length
110 (Bruno and Kennedy, 2000): a minimal patch size is required to reduce water velocity and
111 accumulate fine sediment within plant patches, and the magnitude of these modifications
112 increases with patch length (Bruno and Kennedy, 2000; Bos et al., 2007; Licci et al., 2019).
113 As the changes in biogeochemical processes are linked to the changes in physical conditions
114 (Gutiérrez and Jones, 2006), we hypothesize that the patch length should also influence the
115 magnitude of changes in biogeochemical conditions. Previous studies in rivers focused on the
116 lateral dimension of the scale-dependent feedbacks generated by hydrodynamic forces and
117 erosion and sedimentation processes (Schoelynck et al., 2012), but to our knowledge, the
118 processes operating in the streamwise dimension have not been studied.

119 The objective of this work was, therefore, to investigate how the patch length of
120 submerged aquatic vegetation affects water velocity, sediment characteristics and
121 biogeochemical conditions (i.e., nutrient accumulation/depletion, microbial respiration) in
122 rivers and the consequences for plants. In particular, we investigated the effects of patch
123 length along the streamwise dimension of patches, which have been rarely studied. First, we
124 hypothesized that the effect of patches on within-patch sediment characteristics and
125 biogeochemical conditions would depend on patch length. Thus, for increasing patch length,

126 the flow within the patch and the sediment particle sizes should decrease, while the organic
127 matter content in the sediment accumulations should increase. As a consequence of organic
128 matter accumulation for increasing patch length, the nutrient concentrations should change
129 due to changes in biogeochemical conditions and microbial activities. Second, we hypothesize
130 that plant size depends on patch length and on plant position in the patch, which is a
131 consequence of the changes in velocity, sediment characteristics and nutrient concentrations
132 induced by the plants themselves. To test these hypotheses, we measured flow velocity and
133 sampled sediment and interstitial water in situ along natural patches of *Callitriche platycarpa*
134 of increasing length, measuring characteristics and microbial respiration rates of sediment,
135 nutrient concentrations in the interstitial water, and plant size. Measurements were performed
136 at two sites that differed in mean flow velocity, sediment grain size, and trophic level.

137

138 **2. Materials and methods**

139 *2.1 Study sites and species*

140 The study was conducted in two drainage channels of the Upper Rhône River
141 (France), near Brégner-Cordon (45.6452 N, 5.6080 E, abbreviated to BC) and Serrières-de-
142 Briord (45.8153 N, 5.4269 E, abbreviated to SB) (Licci et al., 2019, Fig. S2, Table S1). These
143 artificial drainage channels, built in the 1970s and 1980s, are fed by Rhône River seepage
144 (groundwater and surface water seeping through the dikes) and hillslope aquifers. They were
145 excavated in alluvial terraces composed of heterogeneous sediment deposits (Teles et al.,
146 2001) that feed the system with fine particles during the wet periods. They present a
147 simplified, homogeneous morphology (cross-section, water depth, sinuosity) and reduced
148 flow variability due to groundwater supplies (Cornacchia et al., 2018). Only during flood
149 events are the channels fed directly by the surface water of the Rhône River overflowing or
150 flowing back into the channels. No flows or low flow periods occurred before the sampling

151 period, and discharges and velocities were stable over time throughout the sampling period
152 (Cornacchia et al., 2018, Fig. S3). The channels are colonized naturally by submerged aquatic
153 vegetation, which is not managed in this part of the Rhône River. The cover by aquatic
154 vegetation ranges from 30% to 90% depending on the season and channel section. The
155 important development of vegetation and simplified channel morphology enables the
156 identification of a large number of plant patches in similar conditions (water depth, velocity,
157 substrate, etc.) over a short reach length (Cornacchia et al., 2018). Working on these sites to
158 investigate plant-flow-sediment interactions represented an improvement over experiments
159 under controlled conditions, such as flume studies, as it allowed the study of well-established
160 vegetation exposed to natural environmental conditions, but with reduced complexity in terms
161 of channel hydromorphology and between patch conditions. At the patch scale, in particular,
162 the physical conditions (water depth and velocity) encountered by the vegetation were
163 relatively homogeneous between patches, enabling the effects of patch length on these
164 interactions to be explored.

165 During summer 2014 (May-July), the water velocity, interstitial water and surficial
166 sediment were characterized upstream of each patch studied (n=5 per channel, cf. §2.2 Field
167 Sampling) following the methods described in §2.3 (Water velocity), 2.4 (Interstitial water)
168 and 2.5 (Sediment). The two sites presented slightly different daily average water velocities,
169 sediment characteristics and nutrient concentrations (Table S1). Depth-averaged and time-
170 averaged velocities on the sampling days were higher in SB than in BC (Table S1). Bare
171 surficial sediments (10 cm deep) in the channels consisted mainly of medium sand for the SB
172 site and fine sand for the BC site, following the Wentworth size classes (Wentworth, 1922).
173 The median particle size of the bare sediments represented by the mean of the percentile
174 values $d_{0.5}$ (i.e., the maximal diameter of the 50% particle volume) was significantly higher in
175 SB than in BC (241.6 and 148.3 μm , respectively, Table S1), and the silt to clay ratio was

176 lower in SB than in BC (3.74 and 6.43, respectively, Table S1). Site SB presented higher
177 surface water concentrations of nitrate than site BC (11.0 and 3.45 ppm, respectively, Table
178 S1).

179 The aquatic plant species *Callitriche platycarpa* Kütz. was studied, as it is abundant in
180 these channels and can form monospecific patches that are often well isolated (Fig. 1a, b,
181 Licci et al., 2019). *C. platycarpa* has densely packed leaves, forming a rosette at the shoot
182 apex and resulting in a large part of the biomass being concentrated in the upper part of the
183 canopy (Sand-Jensen and Mebus, 1996). *C. platycarpa* has thin, flexible, and highly branched
184 stems, 10-200 cm long, forming dense patches (up to $5-10 \times 10^3$ shoots/m²) due to the
185 entanglement of shoots (Fig. 1c, Tison and de Foucault, 2014). Patches of *C. platycarpa*
186 usually present an elliptical structure, and the patch height increases along the patch length
187 (Fig. 1a). Patches over 1 m long are typically only rooted in the upstream section and usually
188 present an overhanging canopy, created by the long, flexible and buoyant stems extending in
189 the downstream direction (Fig. 1b). The patches expand through the growth of the individual
190 plants and through the production of new plants by vegetative multiplication, which occurs
191 mostly at the downstream edge of the patch. At the study sites, patches can persist over winter
192 and reach a length of 3-4 m.

193

194 2.2 Field sampling

195 During summer 2014, five patches of *C. platycarpa* with a maximum reach length of
196 300 m were selected at each site. Selected patches were located as far as possible from the
197 channel banks and from other patches to minimize interference. The five patches per site were
198 selected to encompass the range of patch lengths observed at the two sites (0.16 m to 3.13 m
199 for the BC site and 0.30 m to 2.50 m for the SB site, these lengths reflecting the age of the
200 patches). Patch length (L), width (W) and maximal height (h) were measured with a

201 measuring tape. As W and h were correlated to L (with a log-log relationship between L and
202 W , $r=0.84$, $p<10^{-4}$, and a linear relationship between L and h , $r=0.83$, $p<10^{-4}$), L was chosen
203 as an integrative variable to describe patch size. The dimensions and their ratios for each
204 patch investigated are reported in Table S2.

205 For each patch, water velocity measurements, interstitial water sampling and sediment
206 collection were performed at the same time at five sampling points along its longitudinal axis:
207 4 sampling points inside the patch located at 10%, 30%, 50%, and 90% of canopy length,
208 starting from the leading edge, and one sampling point outside the patch located
209 approximately 1 m upstream from its leading edge (U) (Fig. 2). For each patch, the upstream
210 sampling point was taken as a reference to the local conditions near the patch. At each
211 sampling point, water velocity profile measurements were first performed (details in § 2.3),
212 followed by sampling of interstitial water (details in §2.4) and collection of a sediment core
213 (details in §2.5). Finally, for all patches, plants were harvested at the 2 sampling points
214 located at 10% and 90% of the canopy length (details in §2.6).

215

216 *2.3 Flow velocity measurements*

217 For each sampling point (Fig. 2), a vertical profile of velocity was measured using a
218 3D Acoustic Doppler Velocimeter (ADV, FlowTracker Handheld-ADV, SonTek, USA).
219 Vertical profiles were constructed with depth intervals of less than 12 cm and reduced to 1-4
220 cm near plant-water interfaces (Sand-Jensen, 1998). Due to the dimensions of the side-
221 looking probe, measurements closest to the sediment (bare or within plant patches) were taken
222 at a minimum of 4 cm above the channel bed. Velocity was recorded over 100 s at 1 Hz.
223 Velocity data were filtered to remove spikes (Goring and Nikora, 2002; Mori et al., 2007).
224 The time average (denoted by an overbar) of the streamwise velocity component, \bar{u} , was used
225 to quantify the flow modification induced by plant patches. From each time-averaged velocity

226 profile, the velocity at 20 cm above the bed, \bar{u}_{20} , was estimated by interpolation if not
227 measured. This distance was chosen to avoid bottom interference due to the presence of
228 boulders and cobbles. Moreover, this choice allowed for measurement of the hydrodynamic
229 forces faced by plants during their growth and the development of the patch in relation to the
230 patch architecture. Indeed, due to the plant morphology and patch architecture (i.e., flexibility
231 of stems, patch height that increases along the patch and L/h ratio), measurements at 20 cm
232 depth were located above the canopy for the shortest patches and at the upstream end of long
233 patches. In these cases, \bar{u}_{20} values represent changes in the velocity field due to lateral
234 deflection of flow away from the patch but overestimate flow velocities within the canopy.

235 To examine the effect of a plant patch on flow conditions within the patch relative to
236 upstream conditions, we calculated the fractional difference between the local velocity, \bar{u}_{20} , in
237 the middle of the longitudinal axis of the patch and the velocity upstream of the patch, \bar{u}_{20U}
238 (Licci et al., 2019). That is, for the 50% position, we defined $\Delta\bar{u}_{20} = (\bar{u}_{20} - \bar{u}_{20U}) \times (\bar{u}_{20U})^{-1}$.

239

240 *2.4 Interstitial water characterization*

241 For each sampling point (Fig. 2), interstitial water was sampled with a 60 mL syringe
242 and screened mini-piezometers (1 m long, 1.7 cm diameter, and 5 cm screen length) pushed
243 20 cm deep inside the riverbed sediments using an internal metallic rod (Lefebvre et al., 2005;
244 Dahm et al., 2007). Interstitial water samples were stored in a cool box with ice during the
245 sampling day and then were filtered (Whatman GF/C, 1.2 μm pore size) and placed at 4 °C in
246 a laboratory refrigerator. Filtered interstitial water samples were then analysed within 48
247 hours using standard colorimetric methods to measure ammonium (EPA Method 349, 1997,
248 US Environmental Protection Agency, Washington, DC), orthophosphate (EPA Method -
249 600/4-79-020, 1983), nitrate and nitrite concentrations (EPA Method 352.2, 1993) with an
250 automatic analyser (Easychem Plus; Systea, Anagni, Italy).

251 Finally, for each sampling point, the relative concentrations of ammonium, nitrite, and
252 nitrate were calculated using the sum of these nitrogen forms as the total dissolved inorganic
253 nitrogen concentration in interstitial water (TDIN).

254

255 *2.5 Sediment characterization*

256 *2.5.1 Sediment collection*

257 At each sampling point (Fig. 2), one sediment sample was taken manually using clear
258 Perspex cores (5 cm diameter and 10 cm deep). The excess water was carefully drained off,
259 and the sediment samples were placed in plastic sampling bags separately for each sampling
260 position without preserving the integrity of the cores. After collection, the sediment samples
261 were stored in a cool box with ice during the sampling day and then placed at 4 °C in a
262 laboratory refrigerator for a maximum 24 h period. In the laboratory, sediments from each
263 core were homogenized, and subsamples were collected separately to perform measurements
264 of sediment grain size, organic matter content, microbial respiration rate and total nitrogen
265 and total organic carbon. Measurements of sediment grain size and organic matter content
266 were made on all the sampling positions of all the patches, whereas due to time limitations,
267 the analyses of microbial respiration rate and total nitrogen and total organic carbon were only
268 made on 2 patches per site (the shortest and longest patches of each site, Fig. 2).

269

270 *2.5.2 Sediment grain size*

271 To perform the effective grain size analyses (i.e., for the whole sediment, without
272 removal of organic matter, McCave and Syvitski, 1991; Phillips and Walling, 1999),
273 sediments were wet sieved with distilled water at 1.6 mm, separating the fine and the coarse
274 fraction, and then dried at 70 °C for 48 hours to allow sample preservation until the analyses
275 were completed. Grain size analyses of sediment were performed in the aqueous phase by

276 laser diffractometry using a Malvern Mastersizer 2000 G (diameter range: 0.01-2000 μm).
277 Prior to the measurements, sediments were sonicated for 2 min to destroy the
278 macroaggregated particles formed during the 70 °C drying process (Badin et al., 2009). The
279 results of the analysis are displayed as grain size distribution curves. The curves were
280 transformed into cumulative curves, and the percentile values $d_{0.1}$, $d_{0.3}$, and $d_{0.5}$ were
281 calculated. These values represent the diameters corresponding to 10%, 30%, and 50% of the
282 total particle volume, respectively (for instance, $d_{0.5}$ represents the diameter for which 50% of
283 the particles are smaller, i.e., the median particle diameter). The three values were correlated
284 ($\rho=0.79$, $p<10^{-3}$ for $d_{0.1}$ and $d_{0.3}$; $\rho=0.63$, $p<10^{-3}$ for $d_{0.1}$ and $d_{0.5}$; $\rho=0.94$, $p<10^{-3}$ for $d_{0.3}$ and
285 $d_{0.5}$, Spearman rank correlation), and only the median particle diameter, $d_{0.5}$, was kept for
286 further analyses. Measurements of grain size were conducted in triplicate for each bulk
287 sample, and mean values and standard deviations of $d_{0.5}$ were calculated (Licci et al., 2019).
288 To describe the sediment grain size at each sampling position, we used only the mean value of
289 $d_{0.5}$, as the standard deviation was less than 10%. We expressed the $d_{0.5}$ relative to the value
290 measured at the upstream position ($d_{0.5\text{ U}}$) to obtain the relative value $\Delta d_{0.5}$ for the 50%
291 position only, as $\Delta d_{0.5} = (d_{0.5} - d_{0.5\text{ U}}) \times (d_{0.5\text{ U}})^{-1}$. Complete sediment grain size distributions
292 and silt/clay ratios for each sampling position of each patch are reported in Tables S3 and S4.

293

294 *2.5.3 Sediment organic matter content*

295 The organic matter content was measured for each sediment sample by weight loss
296 after ignition at 550 °C for 2 hours (LOI, Dean, 1974) and expressed as a percentage.
297 Measurements were undertaken in triplicate for each bulk sample, and arithmetic mean values
298 and standard deviations were calculated. For each sampling position, we used only the
299 average value, as the standard deviation was less than 10%.

300

301 *2.5.4 Microbial respiration rate*

302 Within 24 hours of sediment collection, three subsamples of 5 mL of fresh sediment
303 collected from each core were incubated to measure the potential sediment microbial
304 respiration rate ($\mu\text{g (O}_2\text{) h}^{-1}\text{ g}_{\text{dry sed}}^{-1}$). Incubation was carried out using previously acid-
305 washed 125 mL polyethylene bottles sealed by a double cap and filled with surface water
306 from the river collected at the same time and previously saturated in dissolved oxygen.
307 Incubations were performed under controlled conditions (15 °C, dark, and stirring to avoid O₂
308 stratification in bottles) for ca. 15 h. For each subsample, the oxygen consumption was
309 calculated by measuring the O₂ concentration at the beginning and end of the incubation with
310 an optical dissolved oxygen sensor (HQ40D; Hach, Loveland, CO, USA). The dry weight of
311 each subsample was measured by transfer to a previously weighed aluminium cup once the
312 incubation was finished and then dried at 70 °C until a constant weight was reached. Finally,
313 the microbial respiration rate was expressed in μg of dissolved oxygen consumed per hour
314 and g of dry sediment.

315

316 *2.5.5 Carbon to nitrogen ratio (C:N)*

317 The C:N ratios of sediment subsamples were analysed to assess the quality of the
318 organic matter content in the sediment along the patches. Each subsample was finely ground,
319 acidified with HCl (2 mol l⁻¹) and then placed in ultralightweight silver capsules to measure
320 the total nitrogen and total organic carbon with an elemental analyser (FlashEA; Thermo
321 Fisher Scientific, Waltham, MA, USA). The mean C:N ratio (total organic carbon:total
322 nitrogen) of bare and within-patch sediment was then calculated.

323

324 *2.6 Plant morphology*

325 Five specimens of plants were harvested at the 10% and 90% canopy length positions
326 of the 5 patches per site (Fig. 2). Plants were stored in sealed plastic bags saturated with water
327 in a climatically controlled room at 19 °C for a maximum of 48 h until they were analysed.
328 For each plant sampled, we measured plant height (H_{plant}) with a ruler, stretching and laying
329 the plants on a flat surface, and the mean value was calculated from measurements at two
330 different positions in the patch: 10% of patch length and 90% of patch length. Plant height is
331 recognized as a functional trait indicating the response to hydrodynamic stress and nutrient
332 resources in bed sediment (Puijalón et al., 2007) as well as the role played by plants in
333 biogeochemical cycles (Lavorel et al., 2007).

334

335 *2.7 Statistical analyses*

336 The effects of the patches on sediment organic matter content, microbial respiration,
337 nutrient concentrations (i.e., orthophosphate, ammonium, and nitrates), and the relative
338 concentration of dissolved inorganic nitrogen forms in interstitial water were tested using
339 one-sample t tests (one-sided tests) to compare the average value of each variable inside a
340 patch to the relative upstream value. The Welch t test was used to compare the C:N contents
341 of bare and within-patch sediments of a short and a long patch for the two sites.

342 To test how plant height varied with patch length, linear and quadratic models were
343 fitted to the plant height data measured at the 10% and 90% positions for the full range of
344 patches of increasing length ($n=5$). For each site (BC, SB) and position inside patches (10,
345 90%), plant height was used as a response variable, and patch length was used as an
346 explanatory variable. The Quade test was used to compare the mean plant height at the 10%
347 and 90% positions for the full range of patches of different lengths ($n=5$). The Quade test is a
348 non-parametric two-way analysis of variance used for testing small samples and treatments
349 that have large differences in variability (Quade, 1979).

350 For all the tests, the significance level was 0.05.

351

352 **3. Results**

353 *3.1 Effects of patches on flow velocity*

354 At the two river sites, flow velocities (\bar{u}_{20}) in the middle of plant patches with
355 comparable lengths were similar, particularly with velocities between 0.14 and 0.25 m.s⁻¹ for
356 short patches ($L \leq 0.65$ m) and values below 0.08 m.s⁻¹ for the longest patches (Table S3). For
357 short patches ($L \leq 0.65$ m), \bar{u}_{20} was generally unchanged or accelerated ($\Delta\bar{u}_{20} \geq 0$) because the
358 measurement of \bar{u}_{20} was conducted above the canopy for these short patches (Table S3). For
359 longer patches ($L > 0.65$ m), \bar{u}_{20} tended to decrease compared to the upstream position ($\Delta\bar{u}_{20} <$
360 0), with velocities close to zero in the longest patches (Table S3).

361

362 *3.2 Effects of patches on sediment characteristics*

363 At the two sites, for the shortest patches ($L \leq 0.3$ m), $d_{0.5}$ within the patch was
364 comparable to or larger than the upstream value ($\Delta d_{0.5} \geq 0$), while for longer patches ($L > 0.3$
365 m), $d_{0.5}$ within the patch tended to be lower than the upstream value ($\Delta d_{0.5} < 0$; Table S3, Fig.
366 S4). For the BC site, $\Delta d_{0.5}$ was reduced by between -10% and -78% of the $d_{0.5}$ measured at the
367 upstream position for all patches with $L > 0.3$ m (Table S3). For the SB site, $\Delta d_{0.5}$ decreased
368 with patch length for patches up to 0.85 m and was low for longer patches (Table S3, Fig.
369 S5).

370 At both sites, the patches had effects on organic matter content in sediment, differing
371 for patches of increasing length (Fig. 3a, 4a; Table S4). For short patches ($L \leq 0.9$ m), the
372 values of organic matter content in sediment inside the patches were generally not
373 significantly different from those measured at the upstream position (except for the 0.65 m
374 patch at site SB, Fig. 3a, 4a; Table S4). For longer patches ($L > 0.9$ m), the organic matter

375 content in the sediment was significantly higher inside the patches than in the upstream bare
376 sediment (Fig. 3a, 4a; Table S4).

377 For both river sites, the C:N of sediment inside short patches did not significantly
378 differ from that of the bare sediment (Table 1). In contrast, for both sites, the C:N of sediment
379 inside long patches was significantly higher than that of the bare sediment upstream of the
380 patch (Table 1).

381 The respiration rate of sediment measured in short patches ($L=0.30$ m and $L=0.33$ m
382 for BC and SB, respectively) was not significantly different from the respiration rate
383 measured for the bare sediment upstream of the patch (Fig. 5a, c, one sample t test, $t_3=0.48$,
384 $p=0.33$; $t_3=-4.51$, $p=0.98$, for sites BC and SB, respectively). In contrast, for the long patch
385 ($L=2.27$ m) at the BC site, the respiration rate inside the patch was significantly higher than
386 the upstream respiration rate (Fig. 5b; one sample t test, $t_3=4.41$, $p=0.01$). For a long patch
387 ($L=2.50$ m) in site SB, the microbial respiration rate inside the patch was higher only at the
388 10% canopy length position compared to the upstream value, but on average, the respiration
389 rate measured inside the canopy did not significantly differ from the upstream respiration rate
390 (Fig. 5d, one sample t test, $t_3=1.43$, $p=0.12$)

391

392 *3.3 Interstitial water characteristics*

393 At both sites, patches had significant effects on interstitial water characteristics. At site
394 BC, patches had an effect on nutrient concentrations in interstitial water and on ammonium
395 and nitrate concentrations relative to the total dissolved inorganic nitrogen content (TDIN)
396 depending on patch length (Fig. 3; Table S4). For short patches ($L<0.33$ or $L<0.9$ m,
397 according to the parameter), the values of the parameters inside the patches were not
398 significantly different from those measured at the upstream position (Fig. 3 a-e; Table S4).
399 For longer patches ($L\geq 0.33$ or $L\geq 0.9$ m), orthophosphate and ammonium concentrations

400 inside patches were generally significantly higher than in bare sediment, whereas nitrate
401 concentrations were generally significantly lower within the patch (Fig. 3a-d; Table S4). For
402 the shortest patches ($L < 0.9$ m), the relative proportions of the different forms of dissolved
403 inorganic nitrogen were not significantly different inside the patches relative to the upstream
404 position. In contrast, within longer patches, the relative proportions of dissolved inorganic
405 nitrogen forms differed significantly from the upstream position (Fig. 3e, Table S4). Nitrate
406 went from being the predominant form of dissolved inorganic nitrogen (95%-100% of total
407 dissolved inorganic nitrogen) within short patches ($L < 0.9$ m) to being surpassed by
408 ammonium (60-95% of total dissolved inorganic nitrogen) within long patches ($L \geq 0.9$ m; Fig.
409 3e; Table S4). NO_2^- relative concentrations were negligible for all patches (Fig. 3e).

410 At site SB, for all the patches investigated, orthophosphate concentrations in interstitial water
411 were higher inside the patches compared to the upstream concentration (Fig. 4b; Table S4).
412 The ammonium concentration inside patches was not significantly different from the
413 upstream concentration for the shortest patch and was significantly higher for the longer
414 patches (Fig. 4c; Table S4). Due to a high variance in the measurements inside the patches,
415 the nitrate concentration inside patches was generally not significantly different from the
416 upstream concentration (Fig. 4d; Table S4). The relative forms of dissolved inorganic
417 nitrogen presented a pattern close to the one observed in site BC: for the shortest patch, the
418 relative proportions of the different forms of dissolved inorganic nitrogen were not
419 significantly different inside the patch compared to the upstream position, and nitrate was the
420 predominant form of dissolved inorganic nitrogen compared to ammonium (Fig. 4e, Table
421 S4). For longer patches, the relative forms of dissolved inorganic nitrogen were generally
422 significantly different inside the patches compared to the upstream position, and the relative
423 proportion of ammonium tended to increase, whereas the relative concentration of nitrate

424 tended to decrease along the patch from upstream to downstream (Fig. 4e, Table S4). Nitrites
425 were present in low relative concentrations at all positions for all patches (Fig. 4e).

426

427 *3.4 Effect of patch length on plant height*

428 At site BC, the mean plant height (H_{plant}) was not linearly related to patch length but
429 followed a quadratic relationship with a maximum height reached for intermediate length
430 (around $L=1.8$ m), both at the 10% position (Fig. 6a; $R^2 = 0.99$, $p<0.001$) and at the 90%
431 position (Fig. 6b; $R^2=0.98$, $p<0.01$). The plant height at the 90% position did not significantly
432 differ from that at 10% for a patch of increasing length (Quade test, $F_{1,4}=0.015$, $p=0.91$). At
433 site SB, plant height did not present a significant relationship with patch length, at the 10%
434 position (Fig. 6c; $R^2 = 0.15$, $p = 0.52$, linear regression) nor at the 90% position, and plant
435 height was not related to patch length (Fig. 6d; $R^2 = 0.55$, $p = 0.36$, quadratic regression). The
436 plants positioned at 90% of the patch length were significantly longer than the plants
437 collected at the 10% position (Fig. 6c, d; Quade test, $F_{1,4} = 18$, $p = 0.013$). Contrary to site
438 BC, plant height did not reach a clear maximum value.

439

440 **4. Discussion**

441 The present study investigated the effects of patch length on flow velocities,
442 interstitial water quality, and sediment characteristics, which are proxies for biogeochemical
443 processes. The effect of patch length on plant height and the presence of length thresholds that
444 may induce positive or negative feedbacks for plant patches were also investigated. Our
445 results show that patch length, through its effects on flow velocities, can influence
446 biogeochemical conditions. Our findings also indicate that different nutrient conditions
447 compared to bare sediment exist in patches above certain length thresholds and that these
448 thresholds seem to be associated with positive or negative feedbacks to plants.

449

450 *4.1 Patch length, flow velocity and sediment particles*

451 In accordance with our first hypothesis, our results demonstrated that flow velocity
452 and sediment grain size both depended on patch length. For both sites, as observed previously
453 (e.g., Barcelona et al., 2021b), the shortest patches ($L \leq 0.30$ m) showed almost no change in
454 flow velocity and a slight increase in median sediment grain size compared to the upstream
455 position, indicating that the patch had little influence on velocity at the measured depth and
456 led to a coarser sediment texture. This change in the sediment texture may be related to
457 increased turbulence at the leading edge, resulting in enhanced erosion of fine particles
458 (Cotton et al., 2006; Zong and Nepf, 2010; Zong and Nepf, 2011; Licci et al., 2019). For
459 longer patches, the within-patch velocity was always reduced, except for a patch of
460 intermediate length at the BC site, where $\Delta \bar{u}_{20}$ was positive, indicating flow acceleration
461 above the canopy at the depth where velocity was measured. In these patches, the sediment
462 grain size ($d_{0.5}$) was smaller, indicating accumulation of fine sediment, probably due to the
463 reduction in velocity within the patches that favours the sedimentation of smaller particles
464 (Liu and Nepf, 2016; Licci et al., 2019; Biggs et al., 2021). Some modifications of within-
465 patch sediment grain size may also be due to the retention of suspended and bed-transported
466 particles inside plant patches by collision with stems and leaves (Hendriks et al. 2008; Pluntke
467 and Kozerski 2003).

468

469 *4.2 Sediment biogeochemistry*

470 For both sites, in accordance with our first hypothesis, we demonstrated that the sediment
471 characteristics (organic matter content) and nutrient concentrations in interstitial water inside
472 aquatic vegetation patches are dependent on patch length (Sand-Jensen, 1998).

473 At river site BC, the shortest patches sampled ($L \leq 0.9$ m) had little effect on sediment
474 characteristics, whereas for longer patches sampled ($L \geq 2.27$ m), within-patch sediment had an

475 increased organic matter content, orthophosphate and ammonium concentrations and
476 decreased nitrate concentration in interstitial water compared to the upstream position in bare
477 sediment. As a consequence, the relative concentrations of the different forms of dissolved
478 inorganic nitrogen in interstitial water were reversed compared to the upstream position. At
479 the river site SB, a reduced patch effect on sediment characteristics was observed only for the
480 shortest patch sampled ($L=0.3$ m) for organic matter content, ammonium and relative
481 concentration of the different forms of dissolved inorganic nitrogen and was not visible for
482 orthophosphate and nitrate, indicating a minimal length shorter than the shortest patch studied
483 (0.3 m).

484 The organic matter content and nutrient concentrations (orthophosphate and different forms of
485 dissolved inorganic nitrogen) in the interstitial water measured in the *C. platycarpa* patches
486 were comparable to the values measured in sediment underlying dense patches of other
487 submerged macrophyte species (Sand-Jensen, 1998; Wigand et al., 2001; Schneider and
488 Melzer, 2004; Cotton et al., 2006; Schoelynck et al., 2014). The processes that explain these
489 effects of vegetation patches remain questionable. On the one hand, the accumulation of fine
490 sediment rich in organic matter in long patches may stimulate ammonification processes and
491 increase the resulting ammonium concentrations inside sediments (Fig. S1; Dahm et al.,
492 1987). On the other hand, the enrichment of interstitial water with dissolved ammonia and
493 phosphorus associated with a depletion of nitrates may suggest the establishment of anaerobic
494 conditions in patches above a threshold length ($L > 0.9$ m and 0.3 m at the BC and SB sites,
495 respectively). Indeed, the nutrient concentrations measured in long patches were similar to or
496 higher than those measured in the anaerobic zones of lowland streams (Dahm et al., 1987;
497 Shelley et al., 2017). The observed increases in microbial respiration in long patches (see Fig.
498 4) support the hypothesis of a shift from oxic to anoxic conditions due to organic matter
499 decomposition (Sanders et al., 2007), together with the reduction in oxygenated water supply

500 below fine sediment deposits (Dahm et al., 1987; Sand-Jensen, 1998; Bruno and Kennedy,
501 2000; Schulz et al., 2003). This shift from oxic to anoxic conditions may affect the relative
502 importance of nitrification and denitrification inside sediments (Fig. S1; Pretty et al., 2006).
503 In this context, the high concentration and proportion of ammonium suggest that the anoxic
504 conditions induced an inhibition of nitrification or that the ammonium uptake by the plants
505 was too low to compensate for the ammonium produced by ammonification (Ladd and
506 Jackson, 1982; Caffrey and Kemp, 1992; Lefebvre et al., 2004). At the same time, the
507 decreased proportion of nitrates indicates an enhancement of the denitrification processes in
508 sediments with plants (Caffrey and Kemp, 1992; Forshay and Dodson, 2011; Audet et al.,
509 2021). The nitrate uptake by roots is generally low because ammonium uptake is usually
510 preferred in aquatic plants (Nichols and Keeney, 1976; Barko et al., 1991; Xie et al., 2005).
511 The absence or low patch threshold length at site SB suggests that the effect on
512 biogeochemical conditions may be induced even for very short patches, either directly due to
513 the higher trophic level at this site or indirectly, for instance, because of a higher plant
514 density.

515 For long plant patches at both sites, the microbial respiration rate and the mean C:N of
516 the within-patch sediment were higher than the respective mean values measured in the
517 upstream bare sediments, as stated in our first hypothesis. In short patches, the low microbial
518 respiration rate was probably due to the low quantity of organic matter, even if the organic
519 matter was fresh and highly labile (i.e., low C:N, Eskelinen et al., 2009), whereas for long
520 patches, the high microbial respiration rate was likely due to the higher quantity of organic
521 matter. The high microbial activity could also explain the low lability (i.e., high C:N) of the
522 organic matter present in long patches. In long patches, the limited water exchanges, the
523 possible anoxic conditions and the presence of refractory organic matter decelerate the
524 decomposition process (Canfield, 1994; Kristensen et al., 1995), favouring the accumulation

525 of organic matter. These trends observed in patches of *C. platycarpa* do not occur with all
526 species (Caffrey and Kemp, 1992; Forshay and Dodson, 2011). Some species of macrophytes
527 (for example, *Potamogeton crispus*, *Stuckenia pectinata*, *Littorella uniflora*, *Lobelia*
528 *dortmanna*) release oxygen through their roots (Sand-Jensen et al., 1982; Colmer, 2003),
529 enhancing nitrification and buffering the negative effects of anoxia, organic matter, and
530 ammonium toxicity (Lemoine et al., 2012; Soana and Bartoli, 2013). Therefore, the presence
531 of a set of species with different traits and physiologies (e.g., capacity to release oxygen by
532 roots) will likely lead to different biogeochemical processes (as observed in Mermillod-
533 Blondin et al., 2008) and promote the heterogeneity of rivers.

534

535 4.3. Effect of patch length on plant height: feedbacks for plants

536 At site BC, as hypothesized, the heights of plants located at the downstream position
537 of the patch (90% of patch length) were shown to depend on the patch length, and this
538 relationship followed a quadratic pattern. Thus, up to a threshold patch length (approximately
539 1.8 m), plant height increased with patch length but decreased above this threshold,
540 suggesting a negative feedback effect. At site SB, plant height was not related to patch length
541 for either upstream or downstream positions. This could indicate that at this river site with
542 high nutrient content, both in the sediment and in the water, the effect of the patch is already
543 substantial at a short distance from the leading edge of the patch.

544 Plant height represents a functional trait indicating the plant response to hydrodynamic
545 stress and sediment resources (Puijalon et al., 2008; Puijalon et al., 2011) as well as plant
546 effects on biogeochemical cycles (Lavorel et al., 2007). Below a certain patch length, plants
547 are still subjected to hydrodynamic forces, but this has little or no effect on sedimentation
548 (Bruno and Kennedy, 2000), resulting in limited changes in interstitial water nutrient
549 concentrations with reduced feedbacks for the plants. However, with increasing patch length,

550 flow velocities and turbulence are reduced, lowering hydrodynamic stress for the plants
551 (Bruno and Kennedy, 2000; Licci et al., 2019) and promoting the accumulation of sediments
552 and organic matter and increases in nutrient concentrations, resulting in positive feedbacks.
553 Over a certain patch length threshold, the lower plant height may indicate conditions that are
554 less favourable for plants, possibly due to several factors. First, the high ammonium
555 concentration measured in interstitial water of long patches (between 1 and 10 mg l⁻¹ and
556 between 0.4 and 1 mg l⁻¹ for the BC and SB sites, respectively) may induce stress responses
557 and inhibit plant growth, as shown for other aquatic plant species (Britto and Kronzucker,
558 2002; Jampeetong and Brix, 2009, Cao et al., 2004; Cao et al., 2009). The ammonium
559 concentrations measured in long patches of *C. platycarpa* may explain the reduced plant
560 height at site SB and the presence of a threshold length at site BC. Second, the accumulation
561 of ammonium in interstitial water reflects very low concentrations of dissolved oxygen in
562 sediments (Navel et al., 2012), which can be stressful for certain species. Finally, in long
563 patches, photosynthesis may be limited by light limitation induced by self-shading occurring
564 in the region with the highest canopy density (Binzer et al., 2006; Sand-Jensen et al., 2007;
565 Bal et al., 2011). Elucidating the roles of these factors, acting alone or in combination,
566 requires further investigation, for instance by following the dynamics of plant establishment
567 within a patch, growth of individual plants, light attenuation or toxicity on roots in different
568 parts of patches of contrasting sizes.

569

570 *4.4. Consequences for patch dynamics and ecosystem functioning*

571 Our results demonstrate that patch length serves an important role in controlling the
572 effects of patches on flow and sediment deposition, with cascading effects on biogeochemical
573 conditions. These changes in biogeochemical conditions, together with other factors, such as
574 light attenuation due to self-shading occurring in long patches, may play an important role in

575 plant patch dynamics, with positive interactions in patches of short and intermediate lengths
576 and negative interactions in long patches, possibly limiting patch expansion under certain
577 conditions.

578 Previous studies on the effects of patch length on the physical modification of flow
579 and sediment demonstrated that a minimum patch length is required to observe positive
580 feedback for plants (Bruno and Kennedy, 2000), but until now, no maximum length
581 thresholds over which negative feedbacks for plants may occur have been observed when
582 considering hydrodynamic stress alone. This research suggests that it may also be important
583 to also consider nutrient conditions that may induce negative feedback in long patches,
584 limiting their development, together with other factors such as light attenuation due to self-
585 shading.

586 Patterns identified in our study, particularly the threshold length at which changes in
587 flow velocity, sediment characteristics or nutrient conditions occur, may depend on several
588 factors and, primarily, on environmental conditions. In addition to the effect of trophic level
589 suggested by our results, the hydrodynamic conditions of the channels should directly impact
590 the threshold length, both directly and indirectly through the changes in plant morphology
591 induced by flow. In particular, we can hypothesize that, for higher velocity, the threshold will
592 be reached for longer patch length, both due to the higher flow energy and to the smaller size
593 of plants growing in higher flow velocity (Puijalón and Bornette, 2004; Puijalón et al., 2008),
594 resulting in a reduced capacity to attenuate flow. Further studies should investigate threshold
595 lengths in different flow conditions in order to establish general, non-dimensional models
596 predicting thresholds for the modification of sediment properties and nutrient conditions
597 inside patches. Thresholds could also be strongly dependent on plant and patch
598 characteristics, such as the capacity to release oxygen in roots, plant flexibility, and the
599 density of the canopy (Barcelona et al., 2021b; Reitsema et al., 2021), as well as on large-

600 scale canopy organization (Folkard, 2019; Barcelona et al., 2021a). Depending on the
601 morphological and architectural characteristics of plants and patches, it seems plausible that
602 different aquatic plant species will have different effects on hydrodynamics and in turn the
603 characteristics of accumulated sediments, which will induce corresponding effects on
604 biogeochemical conditions, emphasizing the importance of considering plant traits in addition
605 to vegetation biomass alone when studying the role of vegetation at the ecosystem scale (Su et
606 al., 2019; Dalla Vecchia et al., 2020).

607

608 ***5. Conclusion***

609 In conclusion, patches of aquatic plant patches, and in particular patches over a certain
610 length, are biogeochemical hotspots (McClain et al., 2003), with markedly higher rates of
611 some microbial processes involved in nutrient and organic matter recycling. Moreover, the
612 changes in biogeochemical conditions induced by patches may contribute to patch dynamics
613 by limiting plant growth and patch expansion under certain conditions. The autoregulation of
614 patch lengths may maintain ecosystem patchiness and play key roles in ecosystem
615 functioning. Patchiness and the presence of patches of different lengths contribute to the
616 heterogeneity of the ecosystem, with a mosaic of bare sediment and patches with contrasting
617 nutrient conditions leading to possible cascading consequences on the productivity and
618 biodiversity of streams (Dahm et al., 1987). The role of patches in nutrient recycling may also
619 be of interest for applied issues relating, for instance, to wastewater treatment or designing
620 constructed wetlands.

621

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914

915

916 **Figure legends**

917 **Figure 1.** Patch structure and morphology of *C. platycarpa*: (a) frontal and (b) lateral view of
918 long patches ($L > 1$ m), the latter showing an overhanging canopy with only the upstream part
919 of the canopy being anchored in the sediment; (c) a single *C. platycarpa* plant.

920

921 **Figure 2.** Position of the sampling points, number of patches sampled and analyses
922 performed.

923 Five sampling points were defined along the longitudinal axis of each patch: four sampling
924 points were defined along the longitudinal axis of each patch, inside the patch (at 10%, 30%,
925 50%, and 90% of canopy length), and one sampling point was defined outside the patch,
926 approximately 1 m upstream from its leading edge (U). The measurements made (flow
927 velocity, interstitial water, sediment and plant morphology) are listed for each sampling
928 position.

929

930 **Figure 3.** Organic matter content of sediment (a), nutrient concentration in interstitial water
931 (orthophosphates, b, ammonium, c, nitrate, d) and relative forms of dissolved inorganic
932 nitrogen (e) along *Callitriche platycarpa* patches of increasing length at site BC. Sampling
933 positions are explained in Figure 2. Full dots indicate the values measured for sediment within
934 the patches, while empty dots indicate the values measured for the bare sediment at the
935 upstream position (control). Dashed and dotted lines indicate the mean and standard deviation
936 of in-patch values, respectively. Differences between the parameter inside the patch and the
937 relative upstream value: NS, not significant; * $p < 0.05$; ** $p < 0.01$.

938

939 **Figure 4.** Organic matter content of sediment (a), nutrient concentration in interstitial water
940 (orthophosphates, b, ammonium, c, nitrate, d) and relative forms of dissolved inorganic

941 nitrogen (e) along *Callitriche platycarpa* patches of increasing length at site SB. Sampling
942 positions are explained in Figure 2. Full squares indicate the values measured for sediment
943 within the patches, while empty squares indicate the values measured for the bare sediment at
944 the upstream position (control). Dashed and dotted lines indicate the mean and standard
945 deviation of in-patch values, respectively. Differences between the parameter inside the patch
946 and the relative upstream value: NS, not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

947

948 **Figure 5.** Microbial respiration rate along a short patch ($L = 0.3$ to 0.33 m) and a long patch
949 ($L = 2.27$ to 2.50 m) for the two sites, BC and SB. Circles for BC and squares for SB
950 represent the mean value, while error bars represent the standard deviation of the microbial
951 respiration rate for subsamples ($n=3$) of sediment collected in different patch positions.
952 Sampling positions are explained in Figure 2. The horizontal lines indicate the mean and the
953 standard deviation of the sediment respiration rate for the bare sediment upstream of the
954 patch.

955

956 **Figure 6.** Effect of patch length (L) and position (10% and 90%) on plant height (H_{plant}),
957 along patches of *Callitriche platycarpa*, for site BC at the 10% (a) and 90% (b) positions and
958 for site SB at the 10% (c) and 90% (d) positions. Sampling positions are explained in Figure
959 2. Circles for BC and squares for SB represent the mean values, while error bars represent the
960 standard deviation of plant height for specimens ($n=5$) collected in patches of increasing
961 length.

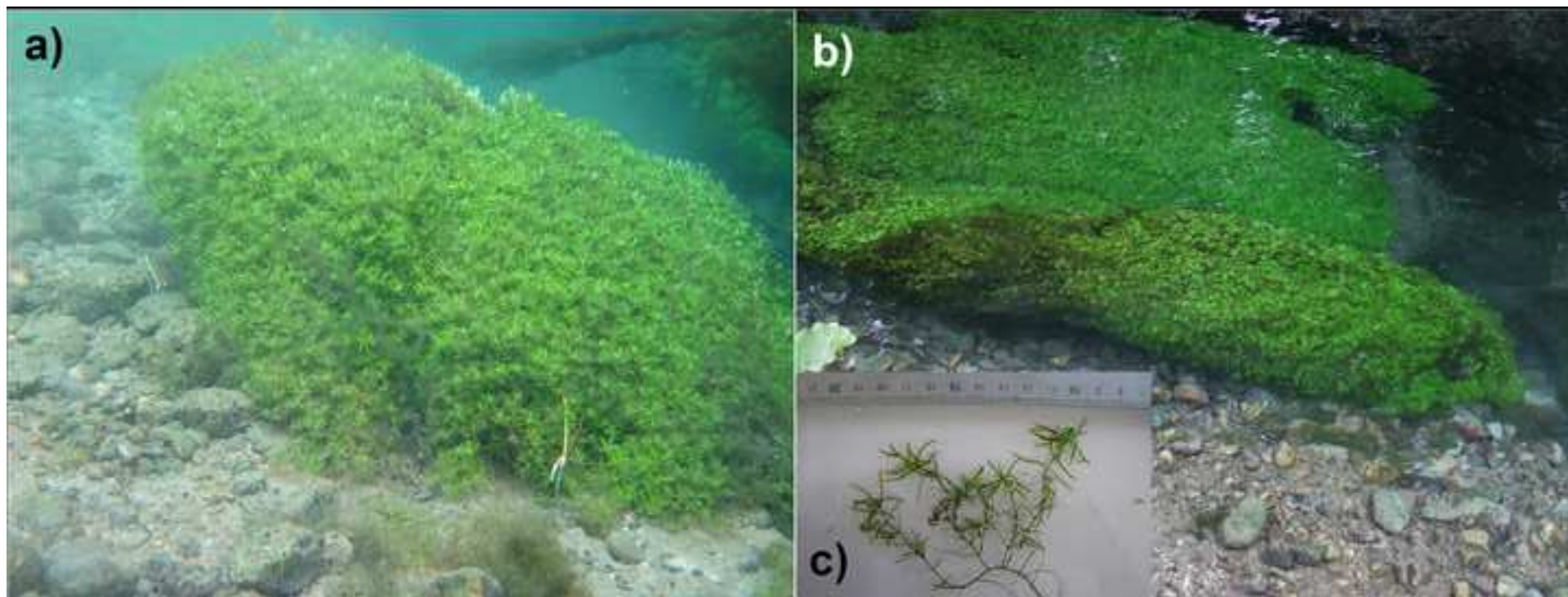
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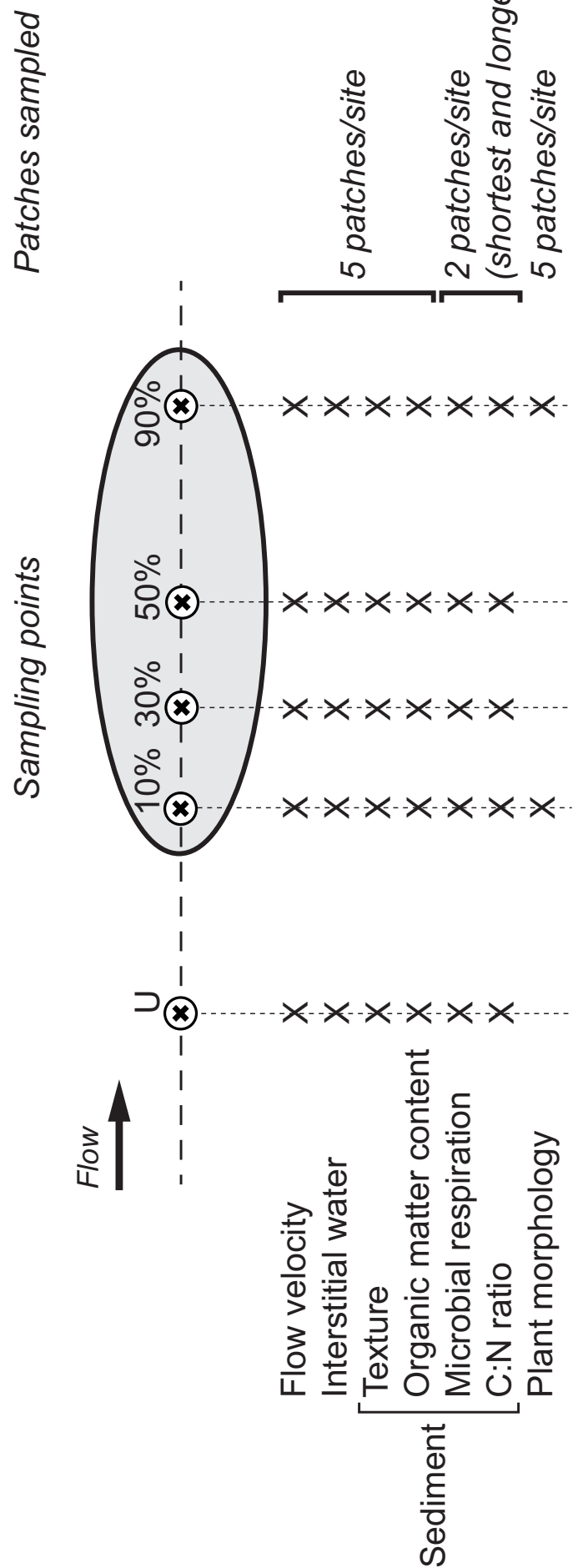
1 **Tables**2 **Table 1.** Comparison of C:N (mean and SD) of sediment in bare sediment and in vegetated

3 sediment for patches of different lengths (Welch t test).

Site	BC				SB			
Patch length	0.33		2.27		0.30		2.50	
L (m)								
Sediment type	Bare	In-patch	Bare	In-patch	Bare	In-patch	Bare	In-patch
Mean C:N	9.74	9.17	7.38	10.89	8.69	7.53	8.69	19.69
± SD	± 0.24	± 0.50	± 0.06	± 0.96	± 0.31	± 1.13	± 0.31	± 5.07
t test (t_{df} ; p)	$t_{3,9}=-1.88$; p= 0.13		$t_{3,1}=7.25$; p=0.005		$t_{2,4}=-1.69$; p=0.21		$t_{3,04}=4.33$; p=0.002	

4





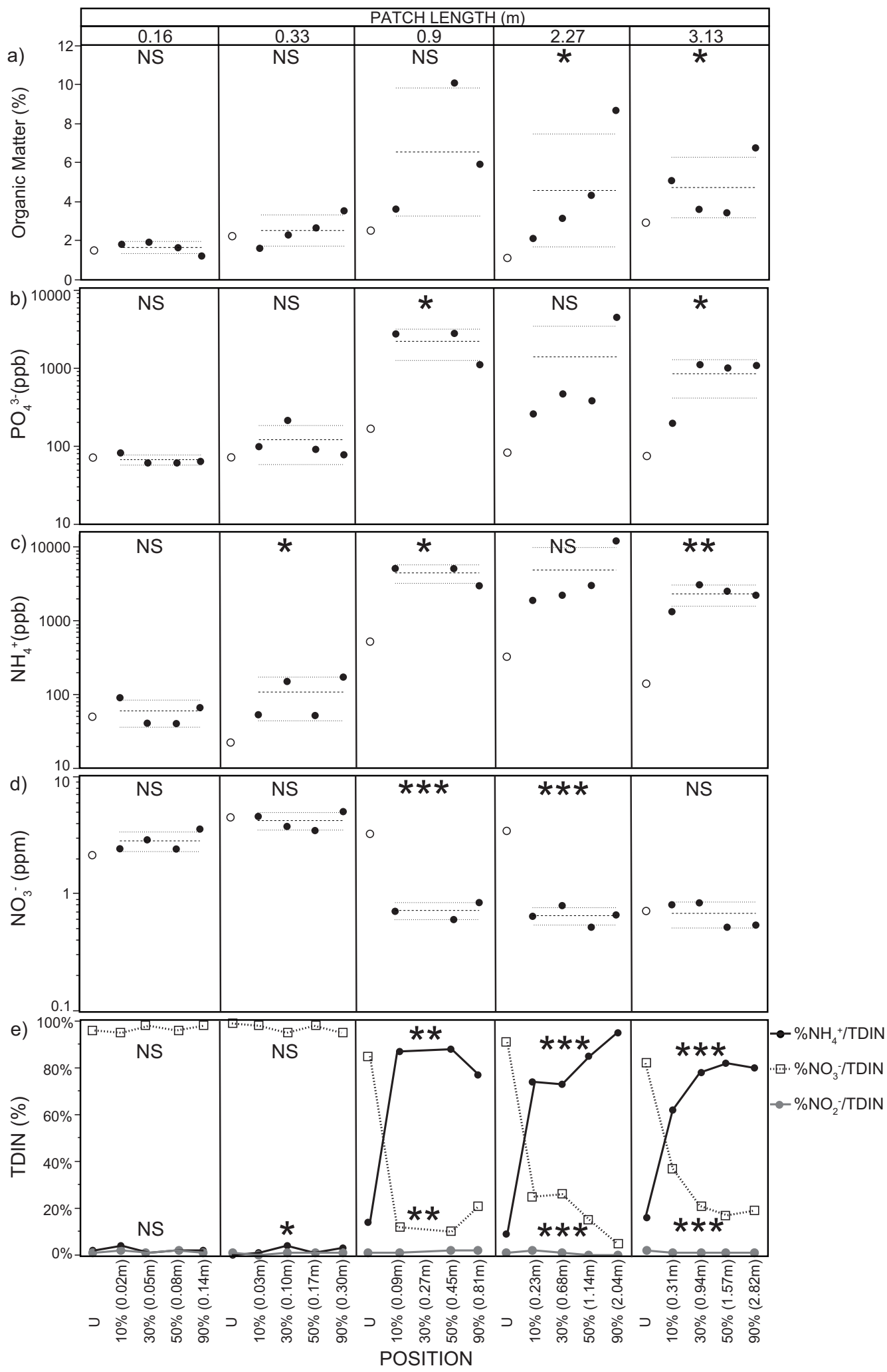
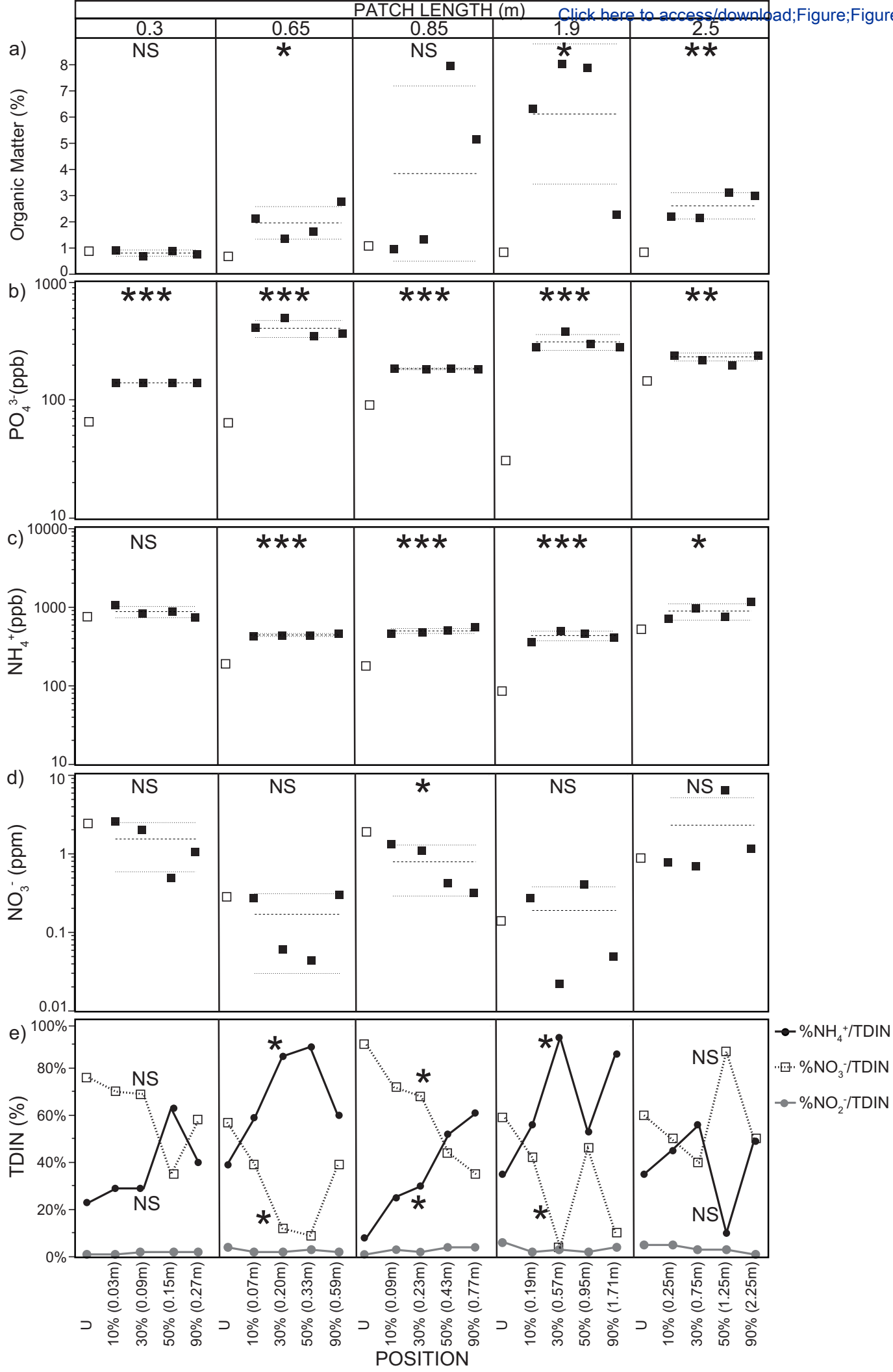
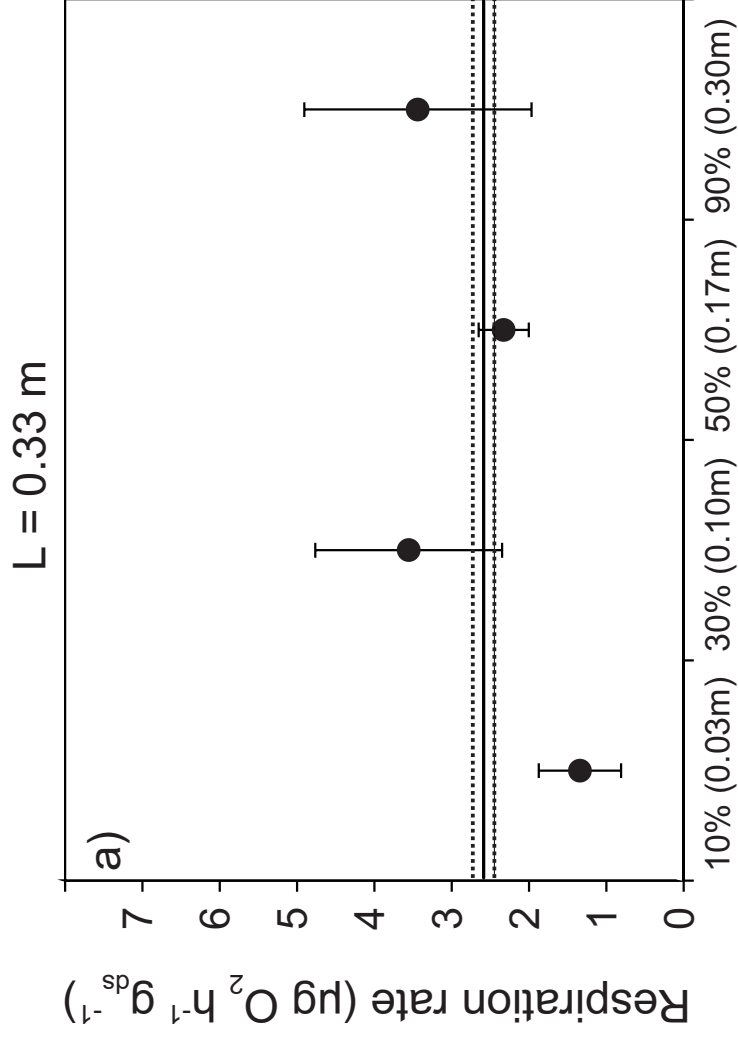
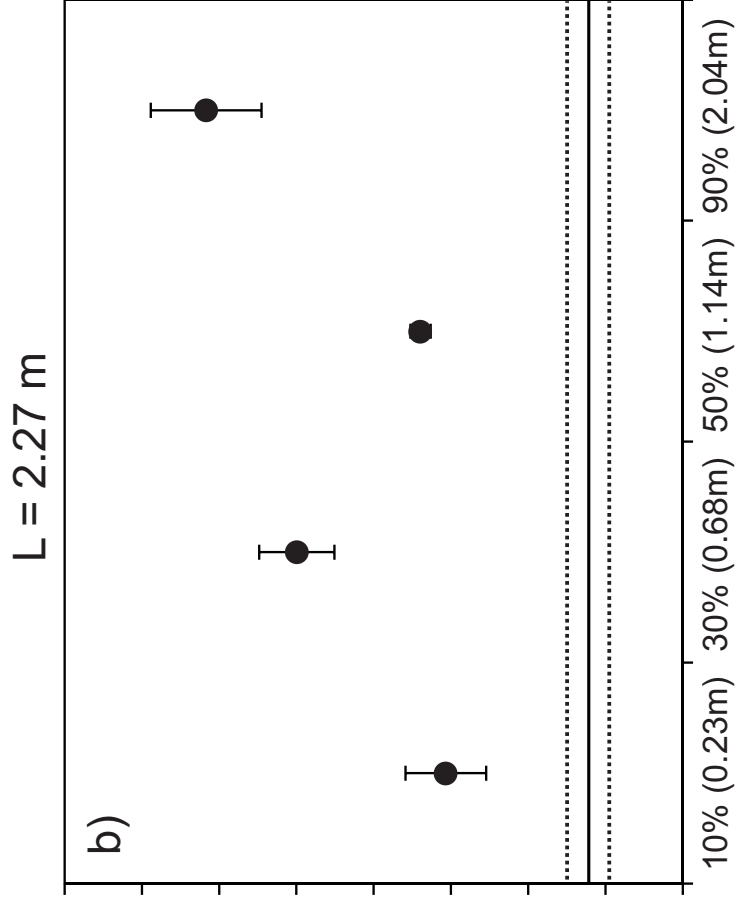


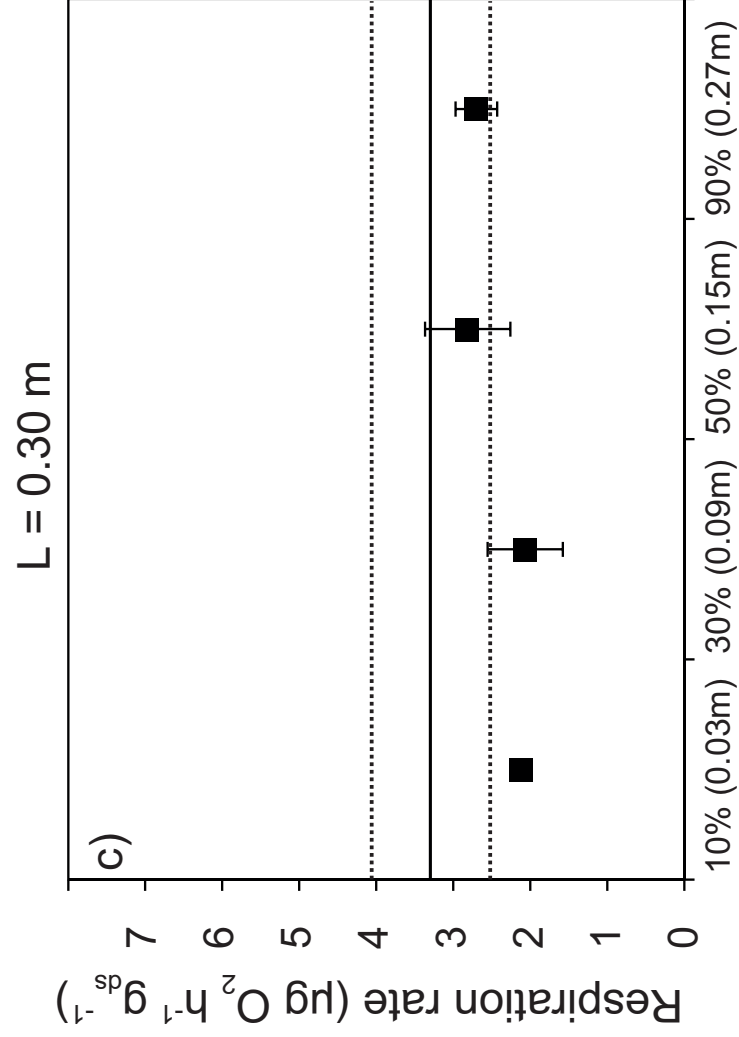
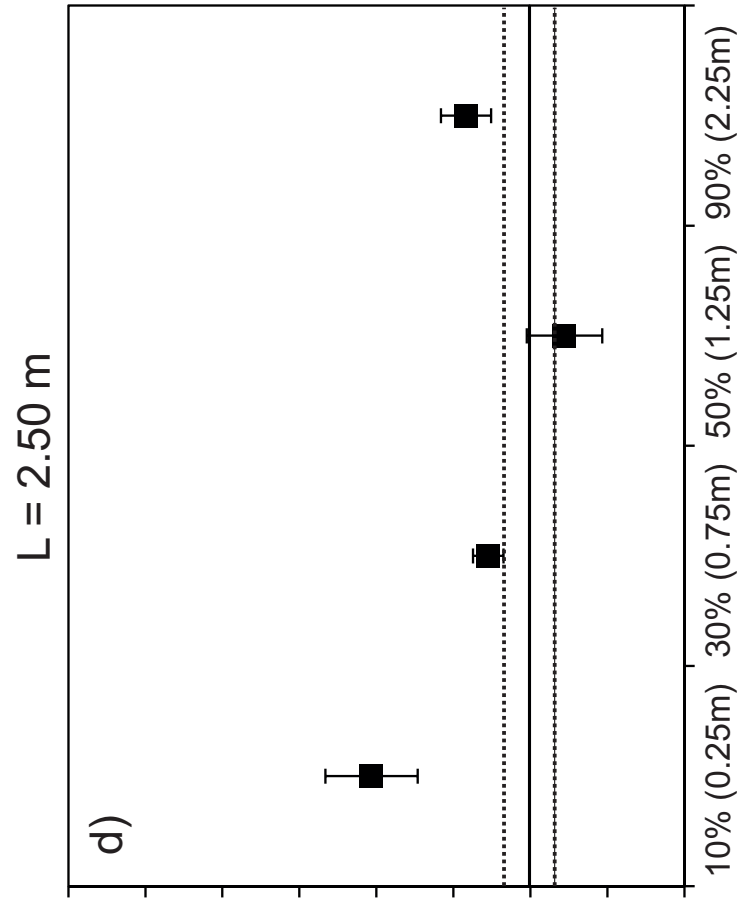
Figure4

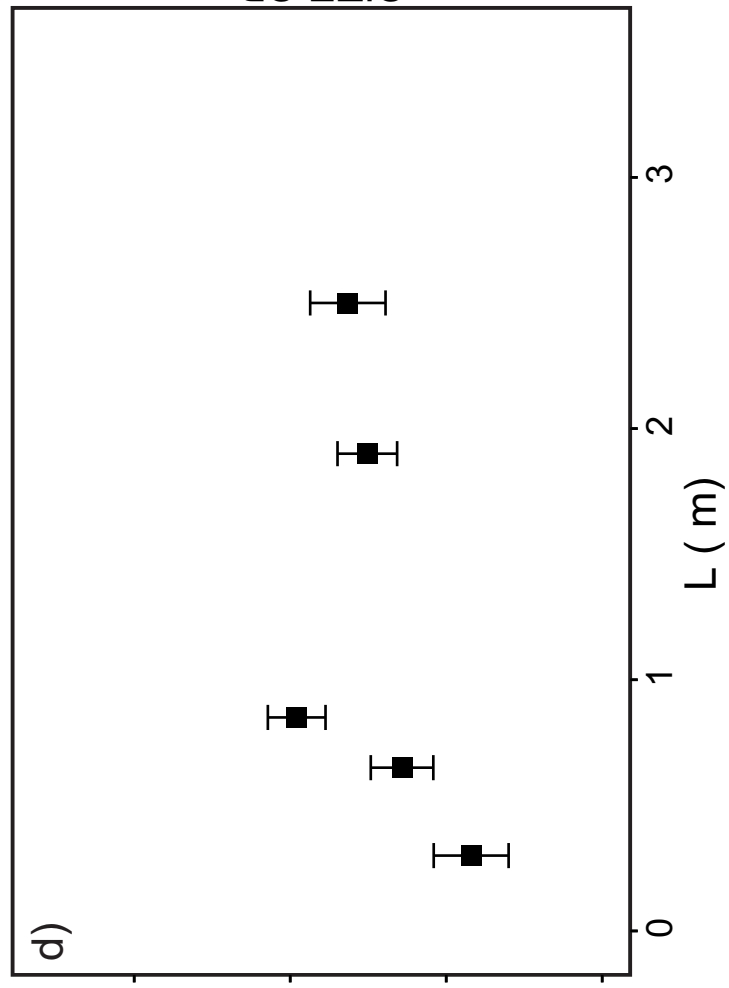
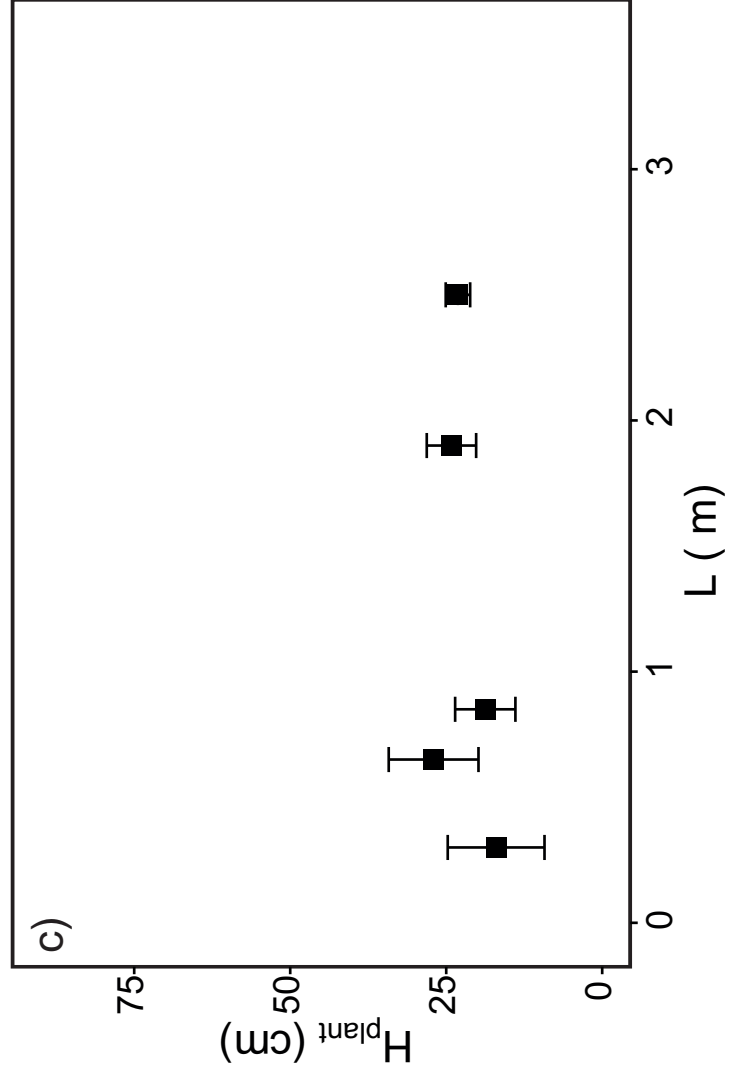
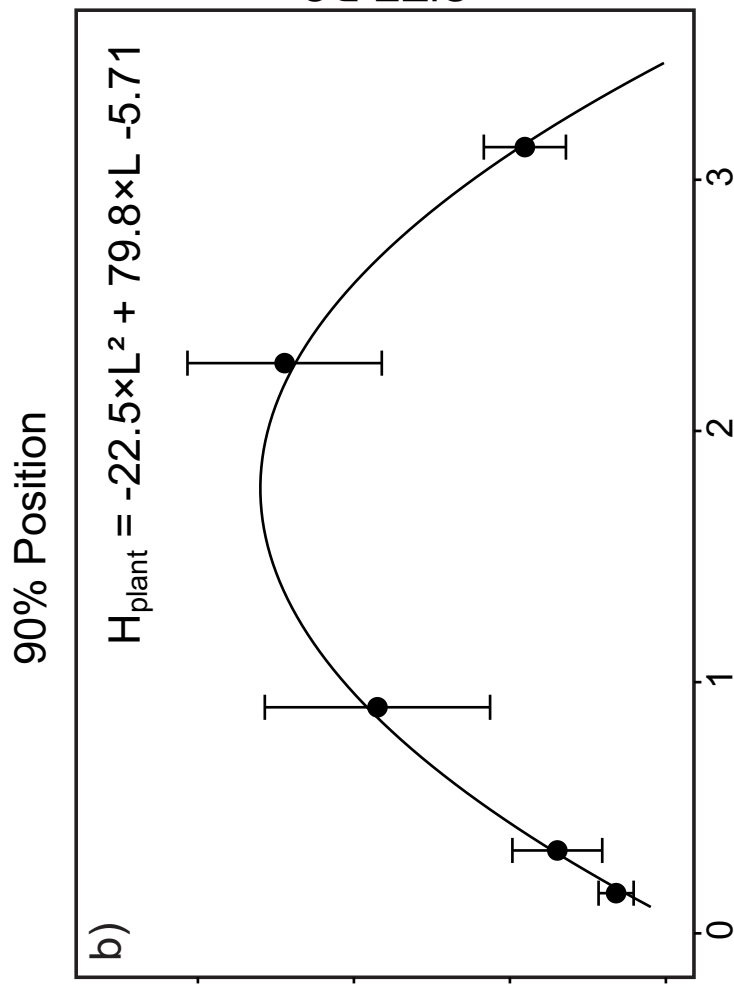
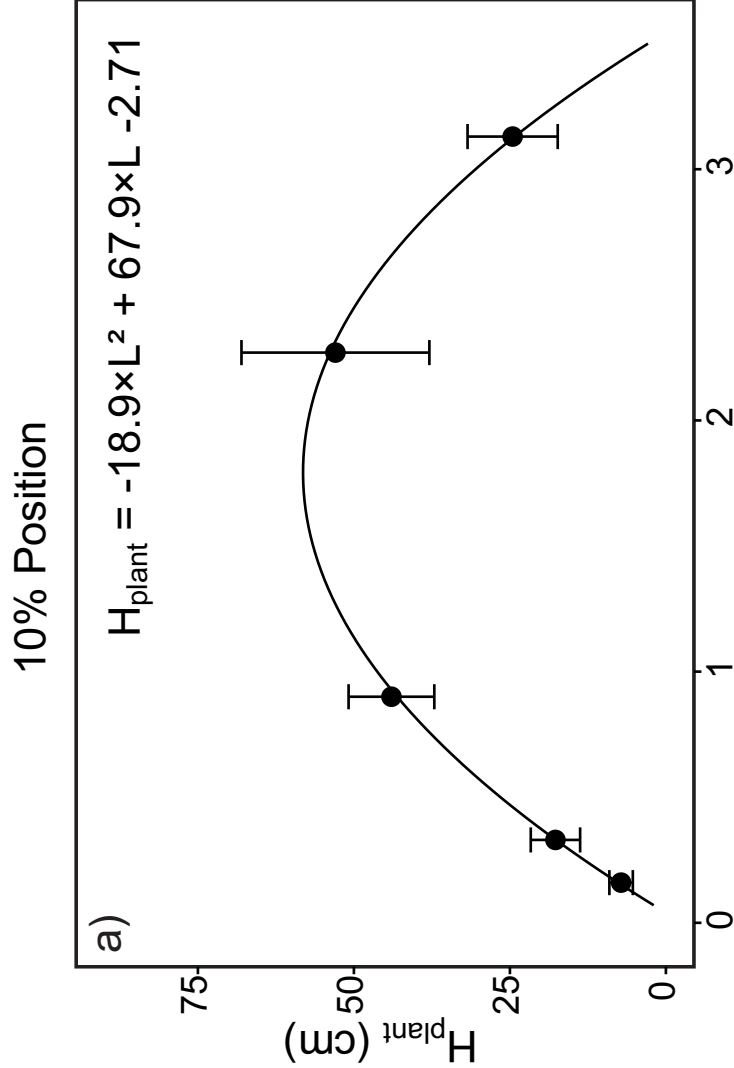
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SITE BC



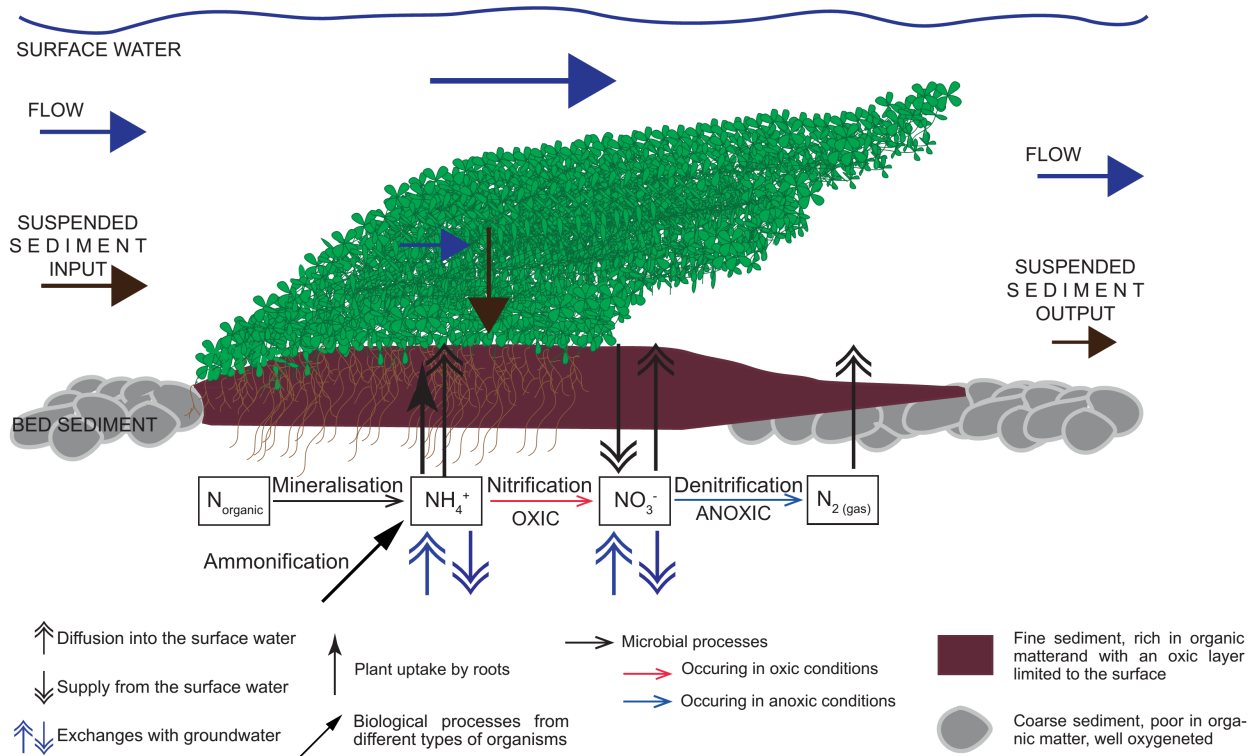
SITE SB





1 **Supplementary Information**

2



3

4

5 **Fig. S1.** Processes regulating the ammonium concentrations in interstitial water under patches

6 of aquatic plants in rivers. The ammonium concentrations in the sediment are controlled

7 firstly by the accumulation of fine sediment and organic material, promoted by the

8 deceleration of flow within plant patches (Sand-Jensen, 1998; Cotton et al., 2005). As fine

9 sediment presents a reduced surface-subsurface water exchange, it is less oxygenated

10 compared to the bare sediment, which is coarser (Findlay, 1995; Morrice et al., 1997).

11 Organic matter contains organic nitrogen that is transformed by bacteria into ammonium by

12 mineralisation. In addition, all organisms produce and release ammonia by ammonification

13 (Ladd and Jackson, 1982). Under oxic conditions ammonium is transformed in nitrates

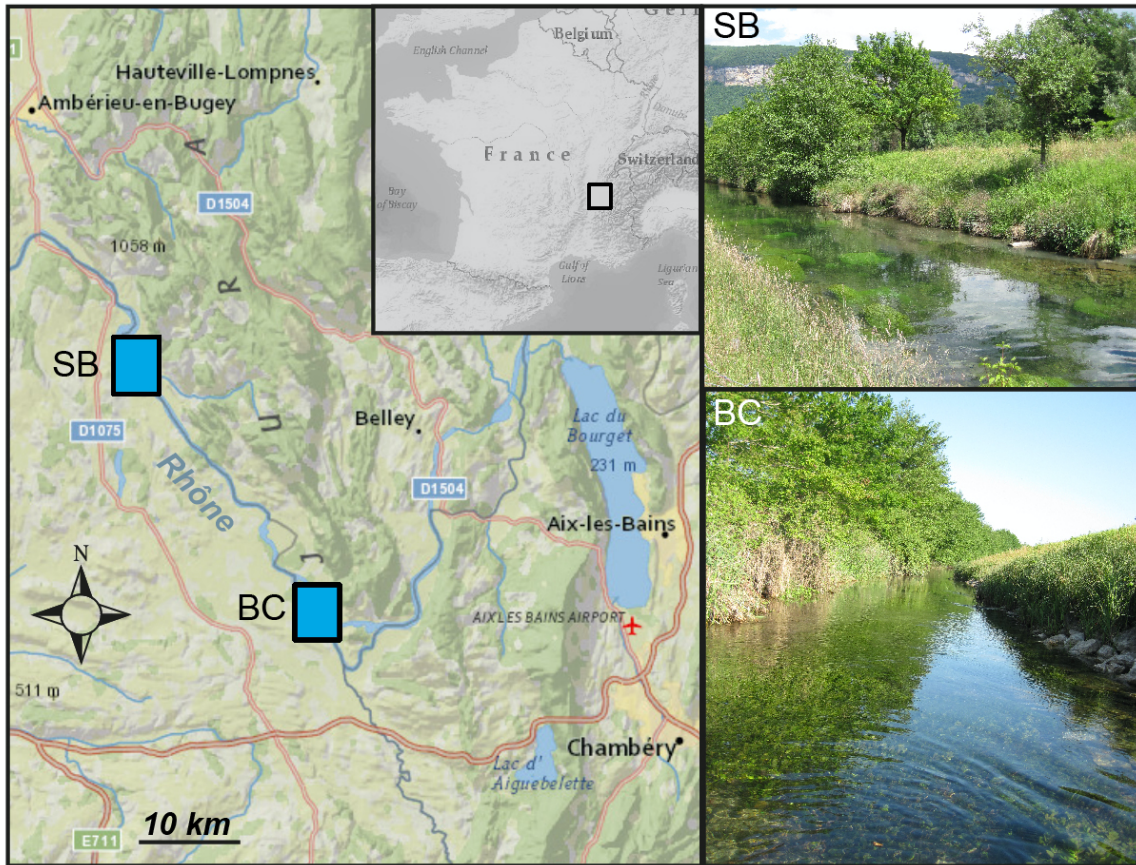
14 through nitrification, this process is limited to the sediment surface in the case of limitation of

15 water exchanges due to fine sediment (Verstraete and Focht, 1977; Schmidt, 1982). Certain

16 aquatic plants are able to release oxygen by root increasing the oxygen availability for
17 nitrifying bacteria, also in deeper sediment (Armstrong, 1971; Lemoine et al., 2012). Under
18 anoxic conditions denitrifying bacteria can transform nitrates in diatomic nitrogen, reducing
19 the nitrogen availability for the system (Verstraete and Focht, 1977; Seitzinger, 1988).
20 Ammonium is the predominant source of nitrogen for aquatic plants, which is followed by
21 nitrates. Due to the higher concentrations of ammonium in the interstitial water compared to
22 the surface water, plants uptake more easily ammonium by roots (Barko and Smart, 1986;
23 Barko et al., 1991). However, high concentrations of ammonium can be toxic for plants
24 (Britto and Kronzucker, 2002; Nimptsch and Pflugmacher, 2007). For this reason, the
25 biogeochemical processes regulating the ammonium concentrations in interstitial water are
26 fundamental for plant growth and survival in rivers.

27

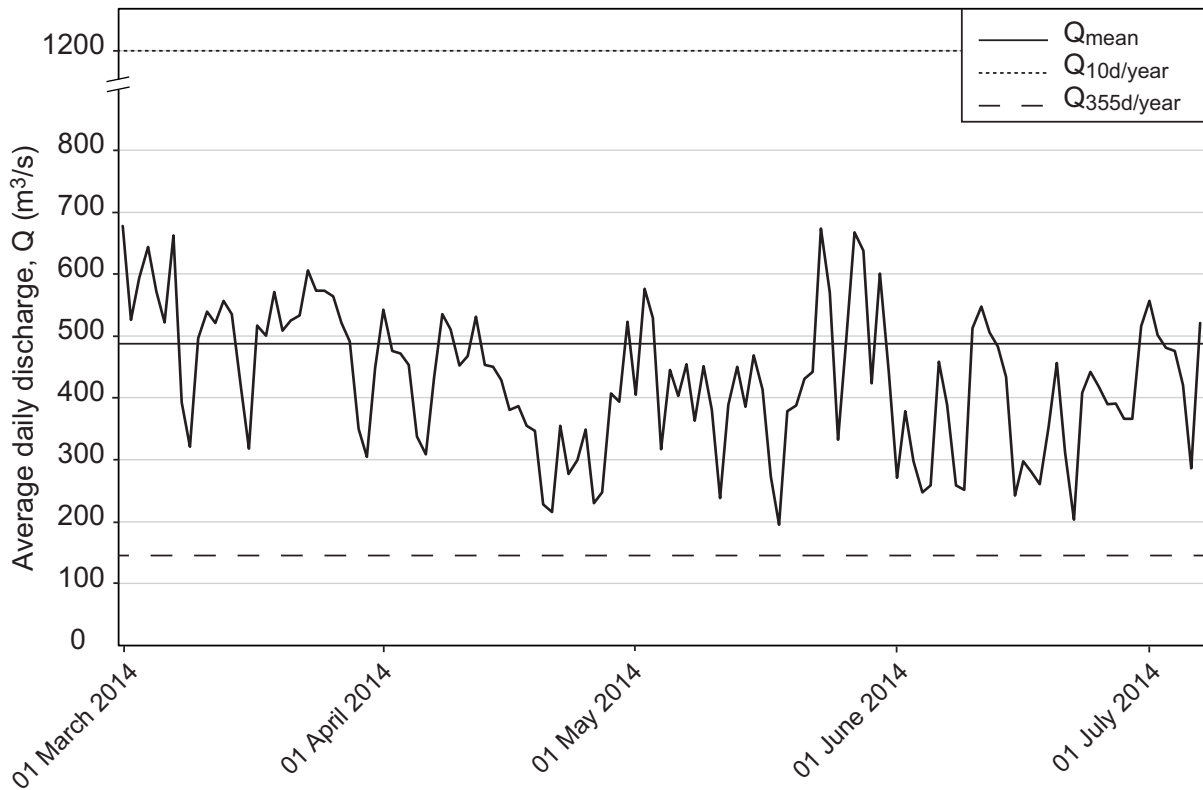
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29

30 **Figure S2.** Location and view of the two sites along the Rhône River, France (SB: Serrières-
31 de-Briord; BC: Brégnier-Cordon).

32



33

34 **Figure S3.** Hydrograph for the period between March and July 2014 for the Rhône River, at

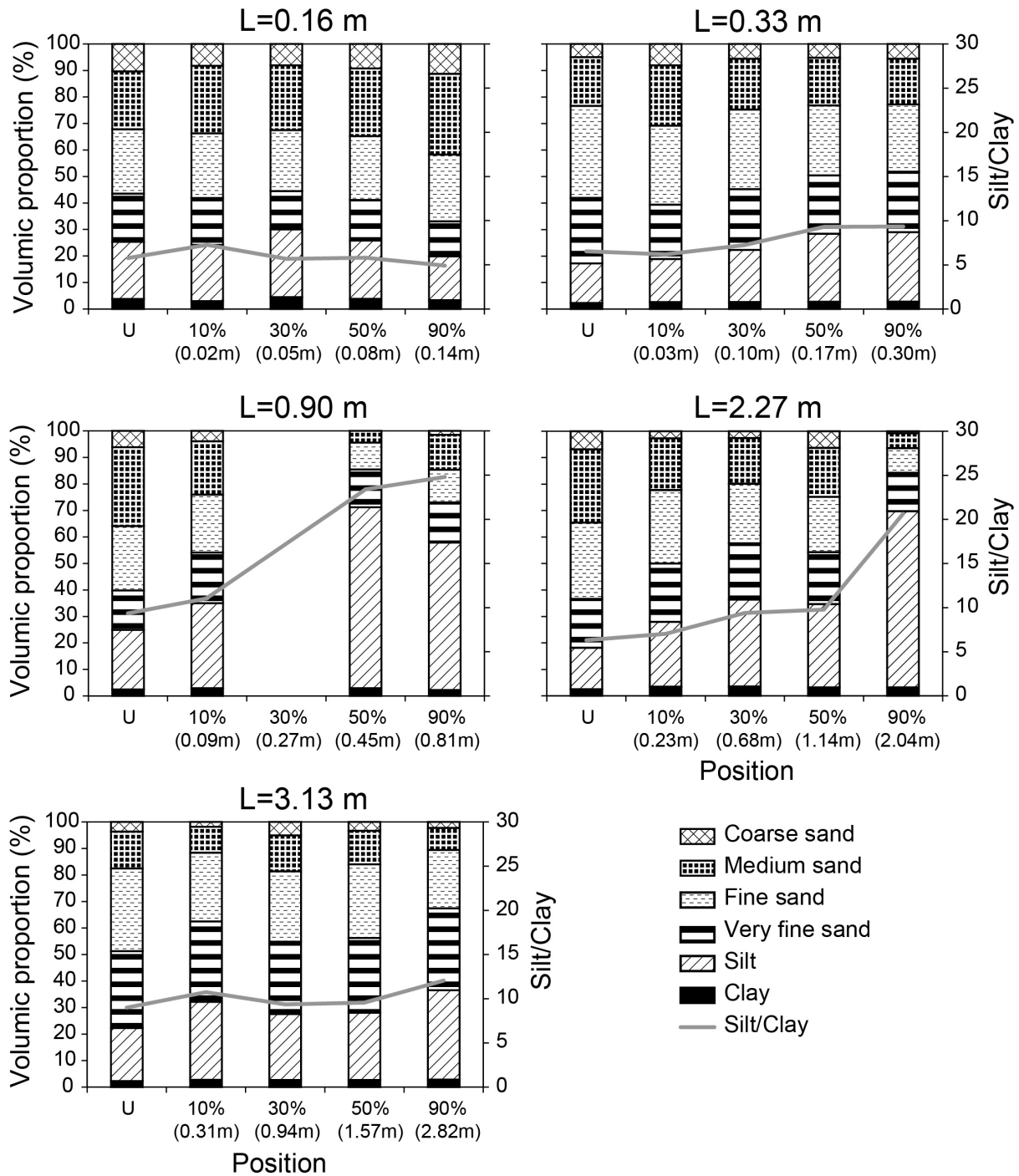
35 Lagnieu (average daily discharge, m³/s). The lines represent the average discharge (Q_{mean},

36 black line), the average daily discharge exceeded 10 days/year (Q_{10d/year}, dotted line) and the

37 average daily discharge exceeded 355 days/year (Q_{355d/year}, dashed line). Data from HYDRO

38 bank (<https://www.hydro.eaufrance.fr/>).

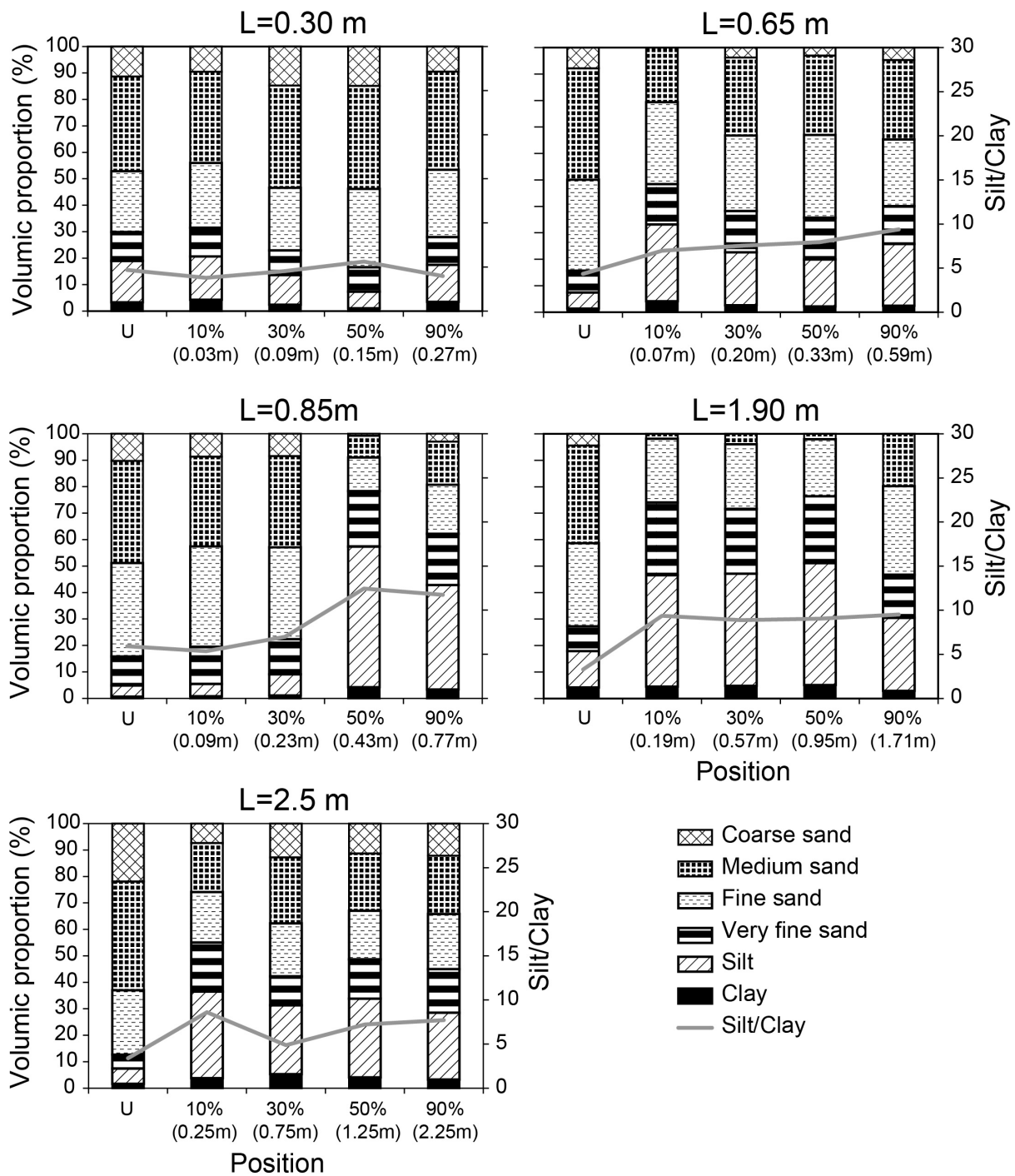
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40

41 **Figure S4.** Sediment grain size distributions and silt to clay ratio at the sampling positions of
 42 the patches of increasing length of *C. platycarpa* at the site BC. Sediment classification
 43 follows the Wentworth size classes (Wentworth, 1922).

44



45

46 **Figure S5.** Sediment grain size distributions and silt to clay ratio at the sampling positions of
 47 the patches of increasing length of *C. platycarpa* at the site SB. Sediment classification
 48 follows the Wentworth size classes (Wentworth, 1922).

49

50 **Table S1.** Description of the two sites: channel geomorphology (maximum channel depth,
51 Z_{Ch} , and width, W_{Ch}), depth-averaged and time-averaged velocity (U), surface water physico-
52 chemical characteristics (conductivity Λ), temperature T , pH, concentration of orthophosphate
53 PO_4^{3-} , ammonium NH_4^+ , nitrate NO_3^- and nitrite NO_2^-), sediment characteristics (median
54 particle size expressed as the percentile value, $d_{0.5}$, organic matter content and the silt to clay
55 ratio) and interstitial water physico-chemical characteristics (concentration of orthophosphate
56 PO_4^{3-} , ammonium NH_4^+ , nitrate NO_3^- and nitrite NO_2^-).

57 The values of velocity, sediment, surface water or interstitial water characteristics are the
58 mean \pm sd of the measurements at the sampling points located upstream of each patch ($n=5$
59 per site). Differences in velocity, sediment, surface water or interstitial water characteristics
60 between sites have been tested with a t-test.

61

		SITE		
		BC	SB	t-test (t_{df} ; p)
Channel morphology	Z_{Ch} (m)	0.8	1.3	
	W_{Ch} (m)	6.0	8.0	
Flow velocity	U (ms^{-1})	0.15 ± 0.02	0.21 ± 0.03	$t_8 = 4.85$; $p=0.001$
	Λ ($\mu S\ cm^{-1}$)	373.1 ± 3.7	443.4 ± 5.0	$t_8 = 25.3$; $p<10^{-4}$
	T ($^{\circ}C$)	13.7 ± 1.2	14.6 ± 0.4	$t_{4.7} = 1.69$; $p=0.15$
	pH	8.0 ± 0.2	8.4 ± 0.2	$t_8 = 1.09$; $p=0.31$
Surface water characteristics	PO_4^{3-} (ppb)	38.5 ± 11.8	48.5 ± 8.8	$t_8 = 1.52$; $p=0.17$
	NH_4^+ (ppb)	16.2 ± 4.8	22.8 ± 7.0	$t_8 = 1.74$; $p=0.11$
	NO_3^- (ppm)	3.45 ± 0.66	11.0 ± 0.65	$t_8 = 18.5$; $p<10^{-4}$
	NO_2^- (ppb)	71.5 ± 79.2	64.7 ± 39.2	$t_8 = -0.17$; $p=0.87$
Sediment characteristics	$d_{0.5}$ (μm)	148.3 ± 21.7	241.6 ± 35.4	$t_8 = 5.03$; $p=0.001$
	Organic Matter (%)	2.07 ± 0.74	0.87 ± 0.14	$t_{4.3} = -3.56$; $p=0.02$

	Silt/Clay	6.43 ± 1.45	3.74 ± 0.94	$t_8 = -3.46 ; p=0.009$
Interstitial water characteristics	PO₄³⁻ (ppb)	94.0 ± 41.6	79.3 ± 42.3	$t_8 = -0.55 ; p=0.60$
	NH₄⁺ (ppb)	213.3 ± 211.3	346.8 ± 284.2	$t_8 = 0.84 ; p=0.42$
	NO₃⁻ (ppm)	2.81 ± 1.44	1.13 ± 1.02	$t_8 = -2.12 ; p=0.07$
	NO₂⁻ (ppb)	33.4 ± 12.9	32.8 ± 27.6	$t_8 = -0.05 ; p=0.96$

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63

64 **Table S2.** Characteristics of environmental conditions (water depth, H) and of *C. platycarpa*
 65 patches measured at BC and SB sites (length L, width W, maximum height h, length to width
 66 ratio L/W, length to height ratio L/h and depth of submergence ratio H/h). Measurements
 67 were taken with a measuring tape.

68

Site	BC					SB				
Patch length L (m)	0.16	0.33	0.90	2.27	3.13	0.30	0.65	0.85	1.90	2.50
W (m)	0.08	0.16	0.50	0.80	0.70	0.10	0.19	0.55	0.84	0.66
h (m)	0.03	0.09	0.10	0.40	0.60	0.02	0.15	0.24	0.46	0.29
L/W	2	2.1	1.8	2.8	4.5	3	3.4	1.5	2.3	3.8
L/h	5.3	3.6	9	5.7	5.2	15	4.3	3.5	4.1	8.6
H (m)	0.48	0.69	0.68	0.51	0.62	0.54	0.57	0.56	0.86	0.55
H/h	16	7.7	6.8	1.3	1.0	27	3.8	2.3	1.9	1.9

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71 **Table S3.** Water velocity (\bar{u}_{20}) and particle size ($d_{0.5}$) measured in the middle of patches of *C.*
72 *platycarpa* of increasing length L (m) in the two sites (BC, SB). Values are reported both as
73 absolute values (\bar{u}_{20} , $d_{0.5}$) and as relatively to the value measured at the upstream position
74 ($\Delta\bar{u}_{20}$, $\Delta d_{0.5}$).

75

Site	BC					SB				
Patch length L(m)	0.16	0.33	0.90	2.27	3.13	0.30	0.65	0.85	1.90	2.50
\bar{u}_{20} (ms ⁻¹)	0.17	0.16	0.14	<0.01	<0.01	0.25	0.14	0.07	<0.01	0.08
$\Delta\bar{u}_{20}$	0.01	0.00	0.22	-1.11	-1.00	0.06	-0.19	-0.69	-0.99	-0.61
$d_{0.5}$ (μm)	159.6	118.8	36.9	104.7	105.4	255.9	171.6	48.9	58.4	127.6
$\Delta d_{0.5}$	0.10	-0.16	-0.78	-0.38	-0.10	0.14	-0.28	-0.79	-0.72	-0.58

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78 **Table S4.** Effect of patch on organic matter content of sediment and nutrient concentrations
 79 in interstitial water for patches of increasing length (tested with one-sided t-tests).

80

Site		BC					SB					
Patch												
length L	(m)	0.16	0.33	0.90	2.27	3.13	0.30	0.65	0.85	1.90	2.50	
Organic	t ₃	0.95	0.72	2.13	2.39	02.32	-1.17	4.10	1.66	3.97	7.11	
Matter	p	0.21	0.26	0.08	0.048	0.05	0.84	0.013	0.10	0.014	0.003	
PO ₄ ³⁻	t ₃	-0.90	1.54	3.70	1.28	3.54	405	10.2	64.2	11.8	8.64	
	p	0.78	0.11	0.03	0.15	0.02	<10 ⁻³	<10 ⁻³	<10 ⁻³	<10 ⁻³	0.002	
NH ₄ ⁺	t ₃	0.79	2.67	5.47	1.8	5.87	1.68	26.5	17.5	11.5	3.58	
	p	0.24	0.04	0.02	0.08	0.005	0.09	<10 ⁻³	<10 ⁻³	<10 ⁻³	0.019	
NO ₃ ⁻	t ₃	2.52	-0.79	-36.7	-49.8	-0.44	-1.96	-1.60	-4.50	0.51	0.99	
	p	0.96	0.24	<10 ⁻³	<10 ⁻³	0.34	0.07	0.10	0.01	0.68	0.80	
%NH ₄ ⁺ /	t ₃	-0.35	2.93	19.9	14.2	12.5	2.09	4.35	3.91	3.54	0.51	
TDIN	p	0.62	0.03	0.001	<10 ⁻³	<10 ⁻³	0.06	0.011	0.015	0.019	0.32	
%NO ₃ ⁻	t ₃	0.07	-2.27	-20.2	-14.9	-12.7	-2.17	-3.96	-3.93	-3.10	-0.29	
/TDIN	p	0.52	0.054	0.001	<10 ⁻³	<10 ⁻³	0.06	0.014	0.015	0.027	0.40	

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