Licci, S.; Marmonier, P.; Wharton, G.; Delolme, C.; Mermillod-Blondin, F.; Simon, L.; Vallier, F.; Bouma, T.J.; Puijalon, S. (2022). Scale-dependent effects of vegetation on flow velocity and biogeochemical conditions in aquatic systems. *Sci. Total Environ. 833*: 155123. DOI: 10.1016/j.scitotenv.2022.155123

Published version: https://dx.doi.org/10.1016/j.scitotenv.2022.155123

NIOZ Repository: http://imis.nioz.nl/imis.php?module=ref&refid=352891

Graphical Abstract

Effect of patch length on physical parameters and nutrient conditions

	Short patch	*Long patch*
Streamwise velocity ($\bar{u}$)	=	-
Sediment grain size (ø)	=	-
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

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

Sofia Licci[a], Pierre Marmonier[a], Geraldene Wharton[b], Cécile Delolme[a, c], Florian Mermillod-Blondin[a], Laurent Simon[a], Félix Vallier[a], Tjeerd J. Bouma[d, e] and Sara Puijalon[a, *]

[1]Univ Lyon, Université Claude Bernard Lyon 1, CNRS, ENTPE, UMR 5023 LEHNA, F-69622, Villeurbanne, France
[b]School of Geography, Queen Mary University of London, London, UK
[c]Univ Lyon, INSA-LYON, DEEP, F-69621 Villeurbanne, France
[d]NIOZ, Royal Netherlands Institute for Sea Research, Department of Estuarine and Delta Systems, and Utrecht University, PO Box 140, 4400 AC Yerseke, The Netherlands
[e]Faculty of Geosciences, Utrecht University, PO Box 80115, 3508 TC Utrecht, The Netherlands

[*]Corresponding author: sara.puijalon@univ-lyon1.fr

Abstract

In rivers, scale-dependent feedbacks resulting from physical habitat modifications control the lateral expansion of submerged plant patches, while the mechanisms that limit patch expansion on a longitudinal dimension remain unknown. Our objective was to investigate the effects of patch length on physical habitat modification (i.e., flow velocity, sediment grain size distribution), the consequences for biogeochemical conditions (i.e., accumulation/depletion of nutrients, microbial respiration), and for individual plants (i.e., shoot length). We measured all of these parameters along natural patches of increasing length. These measurements were performed at two sites that differed in mean flow velocity, sediment grain size, and trophic level. The results showed a significant effect of patch length on organic matter content and nutrient concentrations in interstitial water. For the shortest patches sampled, all of these parameters had similar values to those measured at the upstream control position. For longer patches, organic matter content and orthophosphate and ammonium concentrations increased within the patch compared to the upstream bare sediment, whereas nitrate concentrations decreased, suggesting changes in vertical water exchanges and an increase in anaerobic microbial activities. Furthermore, plant height was related to patch length by a quadratic pattern, probably due reduced hydrodynamic stress occurring for increasing patch length, combined with conditions that are less favourable for plants over a threshold length, possibly due to the light limitation or to the high concentration of ammonium that in the concentration range we measured may be toxic for plants. The threshold lengths over which patches influence the nutrient concentrations were reduced for the site with higher nutrient levels. We demonstrated that the plant-induced modifications of the physical habitat exert important effects on biogeochemical conditions, with possible consequences for patch dynamics and ecosystem functioning.

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

1. Introduction

Physical ecosystem engineers are organisms able to physically modify the abiotic environment, inducing effects for other species or feedbacks for themselves (Jones et al., 1994; 1997). The interaction between the ecosystem engineer and the environment may result in net positive feedback (e.g., stress alleviation or increased availability of resources) or negative feedback (e.g., stress aggravation or reduced availability of resources; Jones et al., 1997; Hastings et al., 2007). When feedbacks are positive at short distances and negative at long distances (i.e., scale-dependent feedbacks), engineering may lead to the formation of regular patterns (or patchiness, Rietkerk and van de Koppel, 2008), as observed, for instance, in bushy vegetation in arid ecosystems (Klausmeier, 1999; Barbier et al., 2006), tussock vegetation in intertidal wetlands (van de Koppel and Crain, 2006), and, recently, submerged aquatic vegetation in rivers (Schoelynck et al., 2012; Cornacchia et al., 2018). In streams, submerged plants typically grow in patches (Fig. 1; Sand-Jensen and Madsen, 1992) and affect ecosystem processes (Carpenter and Lodge, 1986) by modifying flows and sediment dynamics (Wharton et al., 2006; Folkard, 2019). Patches are porous structures through which flow can partially pass, but with a reduced velocity relative to the upstream conditions (Sand-Jensen and Pedersen, 2008; Folkard, 2011; Vandenbruwaene et al., 2011; Nepf, 2012; Marjoribanks et al., 2017; Licci et al., 2019), which causes the flow to deflect and accelerate above and next to the canopy, locally increasing water velocity and turbulence at the edges of the patch (Sand-Jensen and Mebus, 1996; Sand-Jensen and Pedersen, 2008; Sukhodolov and Sukhodolova, 2010; Folkard, 2019). As a result, inside plant patches, the potential for resuspension and erosion is reduced (Sand-Jensen, 1998; Schulz et al., 2003; Hendriks et al., 2009), and fine sediment tends to accumulate compared to bare areas (Cotton et al., 2005; Biggs et al., 2021), whereas flow acceleration next to the patch contributes to particle entrainment and transport (Sand-Jensen, 1998; Schoelynck et al., 2013). As a consequence, plant growth and thus patch expansion could be locally enhanced inside or immediately downstream of a patch due to reduced hydrodynamic stress, a lower risk of mechanical damage for plants (breakage, uprooting) and accumulation of fine particles (Wharton et al., 2006; Jones et al., 2012; Biggs et al., 2021; Reitsema et al., 2021), which in turn increases nitrogen and phosphorus concentrations (Sand-Jensen, 1998; Clarke and Wharton, 2001; Sanders and Trimmer, 2006; Schoelynck et al., 2017) and enhances nutrient availability for plants. Reciprocally, plant growth and thus patch expansion could be inhibited next to the patch due to higher hydrodynamic stress and coarser sediment, leading to the formation of regular patterns (Sand-Jensen, 1998; Schoelynck et al., 2012; Cornacchia et al., 2019).

Ecosystem engineering by aquatic plants also has important implications for biogeochemical processes in rivers (Fig. S1, Gutiérrez and Jones, 2006; Trimmer et al., 2009; Audet et al., 2021). In the case of submerged aquatic plants, the modification of flow and sediment characteristics inside the patches (i.e., reduced flow and grain size) should lead to reduced surface-subsurface water exchange (Findlay, 1995; Morrice et al., 1997), sediment enrichment in organic matter and changes in nutrient concentrations (Dahm et al., 1987; Sand-Jensen, 1998; Schulz et al., 2003; Cotton et al., 2005; Schoelynck et al., 2017). In organic matter-rich sediment, ammonium concentrations increase through mineralization and ammonification (Ladd and Jackson, 1982), and oxygen availability decreases, inducing anaerobic microbial processes (Findlay, 1995; Morrice et al., 1997, Sanders et al., 2007). Under anoxic conditions, denitrifying bacteria can transform nitrates into diatomic nitrogen, reducing the nitrogen availability for the aquatic system (Verstraete and Focht, 1977; Seitzinger, 1988, Gutiérrez and Jones, 2006). Ammonium is the main source of nitrogen for aquatic plants, which is predominant in the interstitial water and assimilated by plant roots (Barko and Smart, 1986; Barko et al., 1991). However, high concentrations of ammonium resulting from high concentrations of sediment organic matter (Barko and Smart, 1983; Sand-Jensen et al., 2005) can inhibit plant growth and photosynthesis (Rudolph and Voigt, 1986; Britto and Kronzucker, 2002; Clarke and Baldwin, 2002; Nimptsch and Pflugmacher, 2007; Cao et al., 2009; Su et al., 2012; Yu et al., 2015). This can induce oxidative stress (Cao et al., 2004; Nimptsch and Pflugmacher, 2007; Cao et al., 2009), lead to internal carbon-nitrogen imbalance (Cao et al., 2009) and even be toxic to plants. Therefore, aquatic plants may influence microbial processes and nutrient availability, inducing positive or negative effects on their own growth (Fig. S1).

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

The objective of this work was, therefore, to investigate how the patch length of submerged aquatic vegetation effects water velocity, sediment characteristics and biogeochemical conditions (i.e., nutrient accumulation/depletion, microbial respiration) in rivers and the consequences for plants. In particular, we investigated the effects of patch length along the streamwise dimension of patches, which have been rarely studied. First, we hypothesized that the effect of patches on within-patch sediment characteristics and biogeochemical conditions would depend on patch length. Thus, for increasing patch length, the flow within the patch and the sediment particle sizes should decrease, while the organic matter content in the sediment accumulations should increase. As a consequence of organic matter accumulation for increasing patch length, the nutrient concentrations should change due to changes in biogeochemical conditions and microbial activities. Second, we hypothesize that plant size depends on patch length and on plant position in the patch, which is a consequence of the changes in velocity, sediment characteristics and nutrient concentrations induced by the plants themselves. To test these hypotheses, we measured flow velocity and sampled sediment and interstitial water in situ along natural patches of *Callitriche platycarpa* of increasing length, measuring characteristics and microbial respiration rates of sediment, nutrient concentrations in the interstitial water, and plant size. Measurements were performed at two sites that differed in mean flow velocity, sediment grain size, and trophic level.

2. Materials and methods

2.1 Study sites and species

The study was conducted in two drainage channels of the Upper Rhône River (France), near Brégnier-Cordon (45.6452 N, 5.6080 E, abbreviated to BC) and Serrières-de-Briord (45.8153 N, 5.4269 E, abbreviated to SB) (Licci et al., 2019, Fig. S2, Table S1). These artificial drainage channels, built in the 1970s and 1980s, are fed by Rhône River seepage (groundwater and surface water seeping through the dikes) and hillslope aquifers. They were excavated in alluvial terraces composed of heterogeneous sediment deposits (Teles et al., 2001) that feed the system with fine particles during the wet periods. They present a simplified, homogeneous morphology (cross-section, water depth, sinuosity) and reduced flow variability due to groundwater supplies (Cornacchia et al., 2018). Only during flood events are the channels fed directly by the surface water of the Rhône River overflowing or flowing back into the channels. No flows or low flow periods occurred before the sampling period, and discharges and velocities were stable over time throughout the sampling period (Cornacchia et al., 2018, Fig. S3). The channels are colonized naturally by submerged aquatic vegetation, which is not managed in this part of the Rhône River. The cover by aquatic vegetation ranges from 30% to 90% depending on the season and channel section. The important development of vegetation and simplified channel morphology enables the identification of a large number of plant patches in similar conditions (water depth, velocity, substrate, etc.) over a short reach length (Cornacchia et al., 2018). Working on these sites to investigate plant-flow-sediment interactions represented an improvement over experiments under controlled conditions, such as flume studies, as it allowed the study of well-established vegetation exposed to natural environmental conditions, but with reduced complexity in terms of channel hydromorphology and between patch conditions. At the patch scale, in particular, the physical conditions (water depth and velocity) encountered by the vegetation were relatively homogeneous between patches, enabling the effects of patch length on these interactions to be explored.

During summer 2014 (May-July), the water velocity, interstitial water and surficial sediment were characterized upstream of each patch studied (n=5 per channel, cf. §2.2 Field Sampling) following the methods described in §2.3 (Water velocity), 2.4 (Interstitial water) and 2.5 (Sediment). The two sites presented slightly different daily average water velocities, sediment characteristics and nutrient concentrations (Table S1). Depth-averaged and time-averaged velocities on the sampling days were higher in SB than in BC (Table S1). Bare surficial sediments (10 cm deep) in the channels consisted mainly of medium sand for the SB site and fine sand for the BC site, following the Wentworth size classes (Wentworth, 1922). The median particle size of the bare sediments represented by the mean of the percentile values $d_{0.5}$ (i.e., the maximal diameter of the 50% particle volume) was significantly higher in SB than in BC (241.6 and 148.3 μm, respectively, Table S1), and the silt to clay ratio was lower in SB than in BC (3.74 and 6.43, respectively, Table S1). Site SB presented higher surface water concentrations of nitrate than site BC (11.0 and 3.45 ppm, respectively, Table S1).

The aquatic plant species *Callitriche platycarpa* Kütz. was studied, as it is abundant in these channels and can form monospecific patches that are often well isolated (Fig. 1a, b, Licci et al., 2019). *C. platycarpa* has densely packed leaves, forming a rosette at the shoot apex and resulting in a large part of the biomass being concentrated in the upper part of the canopy (Sand-Jensen and Mebus, 1996). *C. platycarpa* has thin, flexible, and highly branched stems, 10-200 cm long, forming dense patches (up to 5-10 x10^3 shoots/m^2) due to the entanglement of shoots (Fig. 1c, Tison and de Foucault, 2014). Patches of *C. platycarpa* usually present an elliptical structure, and the patch height increases along the patch length (Fig. 1a). Patches over 1 m long are typically only rooted in the upstream section and usually present an overhanging canopy, created by the long, flexible and buoyant stems extending in the downstream direction (Fig. 1b). The patches expand through the growth of the individual plants and through the production of new plants by vegetative multiplication, which occurs mostly at the downstream edge of the patch. At the study sites, patches can persist over winter and reach a length of 3-4 m.

2.2 Field sampling

During summer 2014, five patches of *C. platycarpa* with a maximum reach length of 300 m were selected at each site. Selected patches were located as far as possible from the channel banks and from other patches to minimize interference. The five patches per site were selected to encompass the range of patch lengths observed at the two sites (0.16 m to 3.13 m for the BC site and 0.30 m to 2.50 m for the SB site, these lengths reflecting the age of the patches). Patch length (L), width (W) and maximal height (h) were measured with a measuring tape. As W and h were correlated to L (with a log-log relationship between L and W, r=0.84, $p<10^{-4}$, and a linear relationship between L and h, r=0.83, $p<10^{-4}$), L was chosen as an integrative variable to describe patch size. The dimensions and their ratios for each patch investigated are reported in Table S2.

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

2.3 Flow velocity measurements

For each sampling point (Fig. 2), a vertical profile of velocity was measured using a 3D Acoustic Doppler Velocimeter (ADV, FlowTracker Handheld-ADV, SonTek, USA). Vertical profiles were constructed with depth intervals of less than 12 cm and reduced to 1-4 cm near plant-water interfaces (Sand-Jensen, 1998). Due to the dimensions of the side-looking probe, measurements closest to the sediment (bare or within plant patches) were taken at a minimum of 4 cm above the channel bed. Velocity was recorded over 100 s at 1 Hz. Velocity data were filtered to remove spikes (Goring and Nikora, 2002; Mori et al., 2007). The time average (denoted by an overbar) of the streamwise velocity component, $\bar{u}$, was used to quantify the flow modification induced by plant patches. From each time-averaged velocity profile, the velocity at 20 cm above the bed, $\bar{u}_{20}$, was estimated by interpolation if not measured. This distance was chosen to avoid bottom interference due to the presence of boulders and cobbles. Moreover, this choice allowed for measurement of the hydrodynamic forces faced by plants during their growth and the development of the patch in relation to the patch architecture. Indeed, due to the plant morphology and patch architecture (i.e., flexibility of stems, patch height that increases along the patch and L/h ratio), measurements at 20 cm depth were located above the canopy for the shortest patches and at the upstream end of long patches. In these cases, $\bar{u}_{20}$ values represent changes in the velocity field due to lateral deflection of flow away from the patch but overestimate flow velocities within the canopy.

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

2.4 Interstitial water characterization

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

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

2.5 Sediment characterization

2.5.1 Sediment collection

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

2.5.2 Sediment grain size

To perform the effective grain size analyses (i.e., for the whole sediment, without removal of organic matter, McCave and Syvitski, 1991; Phillips and Walling, 1999), sediments were wet sieved with distilled water at 1.6 mm, separating the fine and the coarse fraction, and then dried at 70 °C for 48 hours to allow sample preservation until the analyses were completed. Grain size analyses of sediment were performed in the aqueous phase by laser diffractometry using a Malvern Mastersizer 2000 G (diameter range: 0.01-2000 µm). Prior to the measurements, sediments were sonicated for 2 min to destroy the macroaggregated particles formed during the 70 °C drying process (Badin et al., 2009). The results of the analysis are displayed as grain size distribution curves. The curves were transformed into cumulative curves, and the percentile values $d_{0.1}$, $d_{0.3}$, and $d_{0.5}$ were calculated. These values represent the diameters corresponding to 10%, 30%, and 50% of the total particle volume, respectively (for instance, $d_{0.5}$ represents the diameter for which 50% of the particles are smaller, i.e., the median particle diameter). The three values were correlated (ρ=0.79, $p<10^{-3}$ for $d_{0.1}$ and $d_{0.3}$; ρ=0.63, $p<10^{-3}$ for $d_{0.1}$ and $d_{0.5}$; ρ=0. 94, $p<10^{-3}$ for $d_{0.3}$ and $d_{0.5}$, Spearman rank correlation), and only the median particle diameter, $d_{0.5}$, was kept for further analyses. Measurements of grain size were conducted in triplicate for each bulk sample, and mean values and standard deviations of $d_{0.5}$ were calculated (Licci et al., 2019). To describe the sediment grain size at each sampling position, we used only the mean value of $d_{0.5}$, as the standard deviation was less than 10%. We expressed the $d_{0.5}$ relative to the value measured at the upstream position ($d_{0.5\,U}$) to obtain the relative value $\Delta d_{0.5}$ for the 50% position only, as $\Delta d_{0.5} = (d_{0.5} - d_{0.5\,U}) \times (d_{0.5\,U})^{-1}$. Complete sediment grain size distributions and silt/clay ratios for each sampling position of each patch are reported in Tables S3 and S4.

2.5.3 Sediment organic matter content

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

2.5.4 Microbial respiration rate

Within 24 hours of sediment collection, three subsamples of 5 mL of fresh sediment collected from each core were incubated to measure the potential sediment microbial respiration rate (µg (O_2) h^{-1} $g_{\text{dry sed}}^{-1}$). Incubation was carried out using previously acid-washed 125 mL polyethylene bottles sealed by a double cap and filled with surface water from the river collected at the same time and previously saturated in dissolved oxygen. Incubations were performed under controlled conditions (15 °C, dark, and stirring to avoid O_2 stratification in bottles) for ca. 15 h. For each subsample, the oxygen consumption was calculated by measuring the O_2 concentration at the beginning and end of the incubation with an optical dissolved oxygen sensor (HQ40D; Hach, Loveland, CO, USA). The dry weight of each subsample was measured by transfer to a previously weighed aluminium cup once the incubation was finished and then dried at 70 °C until a constant weight was reached. Finally, the microbial respiration rate was expressed in µg of dissolved oxygen consumed per hour and g of dry sediment.

2.5.5 Carbon to nitrogen ratio (C:N)

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

2.6 Plant morphology

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

2.7 Statistical analyses

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

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

For all the tests, the significance level was 0.05.

3. Results

3.1 Effects of patches on flow velocity

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

3.2 Effects of patches on sediment characteristics

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

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

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

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

3.3 Interstitial water characteristics

At both sites, patches had significant effects on interstitial water characteristics. At site BC, patches had an effect on nutrient concentrations in interstitial water and on ammonium and nitrate concentrations relative to the total dissolved inorganic nitrogen content (TDIN) depending on patch length (Fig. 3; Table S4). For short patches (L<0.33 or L<0.9 m, according to the parameter), the values of the parameters inside the patches were not significantly different from those measured at the upstream position (Fig. 3 a-e; Table S4). For longer patches (L≥0.33 or L≥0.9 m), orthophosphate and ammonium concentrations inside patches were generally significantly higher than in bare sediment, whereas nitrate concentrations were generally significantly lower within the patch (Fig. 3a-d; Table S4). For the shortest patches (L<0.9 m), the relative proportions of the different forms of dissolved inorganic nitrogen were not significantly different inside the patches relative to the upstream position. In contrast, within longer patches, the relative proportions of dissolved inorganic nitrogen forms differed significantly from the upstream position (Fig. 3e, Table S4). Nitrate went from being the predominant form of dissolved inorganic nitrogen (95%-100% of total dissolved inorganic nitrogen) within short patches (L<0.9 m) to being surpassed by ammonium (60-95% of total dissolved inorganic nitrogen) within long patches (L≥0.9 m; Fig. 3e; Table S4). NO_2^- relative concentrations were negligible for all patches (Fig. 3e).

At site SB, for all the patches investigated, orthophosphate concentrations in interstitial water were higher inside the patches compared to the upstream concentration (Fig. 4b; Table S4). The ammonium concentration inside patches was not significantly different from the upstream concentration for the shortest patch and was significantly higher for the longer patches (Fig. 4c; Table S4). Due to a high variance in the measurements inside the patches, the nitrate concentration inside patches was generally not significantly different from the upstream concentration (Fig. 4d; Table S4). The relative forms of dissolved inorganic nitrogen presented a pattern close to the one observed in site BC: for the shortest patch, the relative proportions of the different forms of dissolved inorganic nitrogen were not significantly different inside the patch compared to the upstream position, and nitrate was the predominant form of dissolved inorganic nitrogen compared to ammonium (Fig. 4e, Table S4). For longer patches, the relative forms of dissolved inorganic nitrogen were generally significantly different inside the patches compared to the upstream position, and the relative proportion of ammonium tended to increase, whereas the relative concentration of nitrate tended to decrease along the patch from upstream to downstream (Fig. 4e, Table S4). Nitrites were present in low relative concentrations at all positions for all patches (Fig. 4e).

3.4 Effect of patch length on plant height

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

4. Discussion

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

4.1 Patch length, flow velocity and sediment particles

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

4.2 Sediment biogeochemistry

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

At river site BC, the shortest patches sampled (L≤0.9 m) had little effect on sediment characteristics, whereas for longer patches sampled (L≥2.27 m), within-patch sediment had an increased organic matter content, orthophosphate and ammonium concentrations and decreased nitrate concentration in interstitial water compared to the upstream position in bare sediment. As a consequence, the relative concentrations of the different forms of dissolved inorganic nitrogen in interstitial water were reversed compared to the upstream position. At the river site SB, a reduced patch effect on sediment characteristics was observed only for the shortest patch sampled (L=0.3 m) for organic matter content, ammonium and relative concentration of the different forms of dissolved inorganic nitrogen and was not visible for orthophosphate and nitrate, indicating a minimal length shorter than the shortest patch studied (0.3 m).

The organic matter content and nutrient concentrations (orthophosphate and different forms of dissolved inorganic nitrogen) in the interstitial water measured in the *C. platycarpa* patches were comparable to the values measured in sediment underlying dense patches of other submerged macrophyte species (Sand-Jensen, 1998; Wigand et al., 2001; Schneider and Melzer, 2004; Cotton et al., 2006; Schoelynck et al., 2014). The processes that explain these effects of vegetation patches remain questionable. On the one hand, the accumulation of fine sediment rich in organic matter in long patches may stimulate ammonification processes and increase the resulting ammonium concentrations inside sediments (Fig. S1; Dahm et al., 1987). On the other hand, the enrichment of interstitial water with dissolved ammonia and phosphorus associated with a depletion of nitrates may suggest the establishment of anaerobic conditions in patches above a threshold length ($L > 0.9$ m and 0.3 m at the BC and SB sites, respectively). Indeed, the nutrient concentrations measured in long patches were similar to or higher than those measured in the anaerobic zones of lowland streams (Dahm et al., 1987; Shelley et al., 2017). The observed increases in microbial respiration in long patches (see Fig. 4) support the hypothesis of a shift from oxic to anoxic conditions due to organic matter decomposition (Sanders et al., 2007), together with the reduction in oxygenated water supply below fine sediment deposits (Dahm et al., 1987; Sand-Jensen, 1998; Bruno and Kennedy, 2000; Schulz et al., 2003). This shift from oxic to anoxic conditions may affect the relative importance of nitrification and denitrification inside sediments (Fig. S1; Pretty et al., 2006). In this context, the high concentration and proportion of ammonium suggest that the anoxic conditions induced an inhibition of nitrification or that the ammonium uptake by the plants was too low to compensate for the ammonium produced by ammonification (Ladd and Jackson, 1982; Caffrey and Kemp, 1992; Lefebvre et al., 2004). At the same time, the decreased proportion of nitrates indicates an enhancement of the denitrification processes in sediments with plants (Caffrey and Kemp, 1992; Forshay and Dodson, 2011; Audet et al., 2021). The nitrate uptake by roots is generally low because ammonium uptake is usually preferred in aquatic plants (Nichols and Keeney, 1976; Barko et al., 1991; Xie et al., 2005). The absence or low patch threshold length at site SB suggests that the effect on biogeochemical conditions may be induced even for very short patches, either directly due to the higher trophic level at this site or indirectly, for instance, because of a higher plant density.

For long plant patches at both sites, the microbial respiration rate and the mean C:N of the within-patch sediment were higher than the respective mean values measured in the upstream bare sediments, as stated in our first hypothesis. In short patches, the low microbial respiration rate was probably due to the low quantity of organic matter, even if the organic matter was fresh and highly labile (i.e., low C:N, Eskelinen et al., 2009), whereas for long patches, the high microbial respiration rate was likely due to the higher quantity of organic matter. The high microbial activity could also explain the low lability (i.e., high C:N) of the organic matter present in long patches. In long patches, the limited water exchanges, the possible anoxic conditions and the presence of refractory organic matter decelerate the decomposition process (Canfield, 1994; Kristensen et al., 1995), favouring the accumulation of organic matter. These trends observed in patches of *C. platycarpa* do not occur with all species (Caffrey and Kemp, 1992; Forshay and Dodson, 2011). Some species of macrophytes (for example, *Potamogeton crispus, Stuckenia pectinata, Littorella uniflora, Lobelia dortmanna*) release oxygen through their roots (Sand-Jensen et al., 1982; Colmer, 2003), enhancing nitrification and buffering the negative effects of anoxia, organic matter, and ammonium toxicity (Lemoine et al., 2012; Soana and Bartoli, 2013). Therefore, the presence of a set of species with different traits and physiologies (e.g., capacity to release oxygen by roots) will likely lead to different biogeochemical processes (as observed in Mermillod-Blondin et al., 2008) and promote the heterogeneity of rivers.

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

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

Plant height represents a functional trait indicating the plant response to hydrodynamic stress and sediment resources (Puijalon et al., 2008; Puijalon et al., 2011) as well as plant effects on biogeochemical cycles (Lavorel et al., 2007). Below a certain patch length, plants are still subjected to hydrodynamic forces, but this has little or no effect on sedimentation (Bruno and Kennedy, 2000), resulting in limited changes in interstitial water nutrient concentrations with reduced feedbacks for the plants. However, with increasing patch length, flow velocities and turbulence are reduced, lowering hydrodynamic stress for the plants (Bruno and Kennedy, 2000; Licci et al., 2019) and promoting the accumulation of sediments and organic matter and increases in nutrient concentrations, resulting in positive feedbacks. Over a certain patch length threshold, the lower plant height may indicate conditions that are less favourable for plants, possibly due to several factors. First, the high ammonium concentration measured in interstitial water of long patches (between 1 and 10 mg l^{-1} and between 0.4 and 1 mgl^{-1} for the BC and SB sites, respectively) may induce stress responses and inhibit plant growth, as shown for other aquatic plant species (Britto and Kronzucker, 2002; Jampeetong and Brix, 2009, Cao et al., 2004; Cao et al., 2009). The ammonium concentrations measured in long patches of *C. platycarpa* may explain the reduced plant height at site SB and the presence of a threshold length at site BC. Second, the accumulation of ammonium in interstitial water reflects very low concentrations of dissolved oxygen in sediments (Navel et al., 2012), which can be stressful for certain species. Finally, in long patches, photosynthesis may be limited by light limitation induced by self-shading occurring in the region with the highest canopy density (Binzer et al., 2006; Sand-Jensen et al., 2007; Bal et al., 2011). Elucidating the roles of these factors, acting alone or in combination, requires further investigation, for instance by following the dynamics of plant establishment within a patch, growth of individual plants, light attenuation or toxicity on roots in different parts of patches of contrasting sizes.

4.4. Consequences for patch dynamics and ecosystem functioning

Our results demonstrate that patch length serves an important role in controlling the effects of patches on flow and sediment deposition, with cascading effects on biogeochemical conditions. These changes in biogeochemical conditions, together with other factors, such as light attenuation due to self-shading occurring in long patches, may play an important role in plant patch dynamics, with positive interactions in patches of short and intermediate lengths and negative interactions in long patches, possibly limiting patch expansion under certain conditions.

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

Patterns identified in our study, particularly the threshold length at which changes in flow velocity, sediment characteristics or nutrient conditions occur, may depend on several factors and, primarily, on environmental conditions. In addition to the effect of trophic level suggested by our results, the hydrodynamic conditions of the channels should directly impact the threshold length, both directly and indirectly through the changes in plant morphology induced by flow. In particular, we can hypothesize that, for higher velocity, the threshold will be reached for longer patch length, both due to the higher flow energy and to the smaller size of plants growing in higher flow velocity (Puijalon and Bornette, 2004; Puijalon et al., 2008), resulting in a reduced capacity to attenuate flow. Further studies should investigate threshold lengths in different flow conditions in order to establish general, non-dimensional models predicting thresholds for the modification of sediment properties and nutrient conditions inside patches. Thresholds could also be strongly dependent on plant and patch characteristics, such as the capacity to release oxygen in roots, plant flexibility, and the density of the canopy (Barcelona et al., 2021b; Reitsema et al., 2021), as well as on large-scale canopy organization (Folkard, 2019; Barcelona et al., 2021a). Depending on the morphological and architectural characteristics of plants and patches, it seems plausible that different aquatic plant species will have different effects on hydrodynamics and in turn the characteristics of accumulated sediments, which will induce corresponding effects on biogeochemical conditions, emphasizing the importance of considering plant traits in addition to vegetation biomass alone when studying the role of vegetation at the ecosystem scale (Su et al., 2019; Dalla Vecchia et al., 2020).

5. Conclusion

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

Acknowledgements

We thank Leslie Blazere, Vanessa Gardette, Myriam Hammada and Youssouf Sy for field and laboratory assistance and the Compagnie Nationale du Rhône (CNR) for access to field sites. This research was supported by the Research Executive Agency through the 7th Framework Programme of the European Union, Support for Training and Career Development of Researchers (Marie Curie - FP7-PEOPLE-2012-ITN), which funded the Initial Training Network (ITN) HYTECH ‘Hydrodynamic Transport in Ecologically Critical Heterogeneous Interfaces’, N.316546. This study was conducted under the aegis of Rhône Basin Long-Term Environmental Research (ZABR, Zone Atelier Bassin du Rhône) and of the École Universitaire de Recherche H2O'Lyon (ANR-17-EURE-0018).

The authors would like to thank the Associate Editor and five anonymous reviewers for their helpful comments on the manuscript.

References

Audet J, Olsen TM, Elsborg T, Baattrup-Pedersen A, Riis T. 2021. Influence of plant habitats on denitrification in lowland agricultural streams. Journal of Environmental Management, 286: 8.

Badin A-L, Méderel G, Béchet B, Borschneck D, Delolme C. 2009. Study of the aggregation of the surface layer of Technosols from stormwater infiltration basins using grain size analyses with laser diffractometry. Geoderma, 153: 163-171.

Bal KD, Bouma TJ, Buis K, Struyf E, Jonas S, Backx H, Meire P. 2011. Trade-off between drag reduction and light interception of macrophytes: comparing five aquatic plants with contrasting morphology. Functional Ecology, 25: 1197-1205.

Barbier N, Couteron P, Lejoly J, Deblauwe V, Lejeune O. 2006. Self- organized vegetation patterning as a fingerprint of climate and human impact on semi- arid ecosystems. Journal of Ecology, 94: 537-547.

Barcelona A, Colomer J, Soler M, Gracias N, Serra T. 2021a. Meadow fragmentation influences *Posidonia oceanica* density at the edge of nearby gaps. Estuarine Coastal and Shelf Science, 249: 7.

Barcelona A, Oldham C, Colomer J, Serra T. 2021b. Functional dynamics of vegetated model patches: The minimum patch size effect for canopy restoration. Science of the Total Environment, 795: 10.

Barko JW, Gunnison D, Carpenter SR. 1991. Sediment interactions with submersed macrophyte growth and community dynamics. Aquatic Botany, 41: 41-65.

Barko JW, Smart RM. 1983. Effects of organic matter additions to sediment on the growth of aquatic plants. Journal of Ecology, 71: 161-175.

Barko JW, Smart RM. 1986. Sediment- related mechanisms of growth limitation in submersed macrophytes. Ecology, 67: 1328-1340.

Biggs HJ, Haddadchi A, Hicks DM. 2021. Interactions between aquatic vegetation, hydraulics and fine sediment: A case study in the Halswell River, New Zealand. Hydrological Processes, 35: 19.

Binzer T, Sand-Jensen K, Middelboe AL. 2006. Community photosynthesis of aquatic macrophytes. Limnology and Oceanography, 51: 2722-2733.

Bos AR, Bouma TJ, de Kort GLJ, van Katwijk MM. 2007. Ecosystem engineering by annual intertidal seagrass beds: sediment accretion and modification. Estuarine, Coastal and Shelf Science, 74: 344-348.

Britto DT, Kronzucker HJ. 2002. NH_4^+ toxicity in higher plants: a critical review. Journal of Plant Physiology, 159: 567-584.

Bruno JF, Kennedy CW. 2000. Patch-size dependent habitat modification and facilitation on New England cobble beaches by *Spartina alterniflora*. Oecologia, 122: 98-108.

Caffrey JM, Kemp WM. 1992. Influence of the submersed plant, *Potamogeton perfoliatus,* on nitrogen cycling in estuarine sediments. Limnology and Oceanography, 37: 1483-1495.

Canfield DE. 1994. Factors influencing organic carbon preservation in marine sediments. Chemical Geology, 114: 315-329.

Cao T, Ni L, Xie P. 2004. Acute biochemical responses of a submersed macrophyte, *Potamogeton crispus* L., to high ammonium in an aquarium experiment. Journal of Freshwater Ecology, 19: 279-284.

Cao T, Xie P, Li Z, Ni L, Zhang M, Xu J. 2009. Physiological stress of high NH_4^+ concentration in water column on the submersed macrophyte *Vallisneria natans* L. Bulletin of environmental contamination and toxicology, 82: 296-299.

Carpenter SR, Lodge DM. 1986. Effects of submerged macrophytes on ecosystem processes. Aquatic Botany, 26: 341-370.

Clarke E, Baldwin AH. 2002. Responses of wetland plants to ammonia and water level. Ecological Engineering, 18: 257-264.

Clarke SJ, Wharton G. 2001. Sediment nutrient characteristics and aquatic macrophytes in lowland English rivers. Science of The Total Environment, 266: 103-112.

Colmer TD. 2003. Long-distance transport of gases in plants: a perspective on internal aeration and radial oxygen loss from roots. Plant, Cell & Environment, 26: 17-36.

Cornacchia L, Folkard A, Davies G, Grabowski RC, van de Koppel J, van der Wal D, Wharton G, Puijalon S, Bouma TJ. 2019. Plants face the flow in V formation: A study of plant patch alignment in streams. Limnology and Oceanography, 64: 1087-1102.

Cornacchia L, van de Koppel J, van der Wal D, Wharton G, Puijalon S, Bouma TJ. 2018. Landscapes of facilitation: how self-organized patchiness of aquatic macrophytes promotes diversity in streams. Ecology, 99: 832-847.

Cotton JA, Heppell CM, Wharton G, Bass JA. 2005. In-channel storage of fine sediment in vegetated rivers: implications for catchment sediment budgets. Materials and Geoenvironment, 52: 200.

Cotton JA, Wharton G, Bass JAB, Heppell CM, Wotton RS. 2006. The effects of seasonal changes to in-stream vegetation cover on patterns of flow and accumulation of sediment. Geomorphology, 77: 320-334.

Dahm CN, Trotter EH, Sedell JR. 1987. Role of anaerobic zones and processes in stream ecosystem productivity. In: Averett RC, McKnight DM, editors. Chemical Quality of Water and the Hydrologic Cycle. Lewis Publishers, Inc., Chelsea, Michigan, pp. 157-178.

Dahm CN, Valett HM, Baxter CV, Woessner W. 2007. Hyporheic zones. In: Hauer FR, Lamberti GA, editors. Methods in stream ecology. Academic Press, Burlington, MA, pp. 119-142.

Dalla Vecchia A, Villa P, Bolpagni R. 2020. Functional traits in macrophyte studies: Current trends and future research agenda. Aquatic Botany, 167: 13.

Dean WE. 1974. Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition; comparison with other methods. Journal of Sedimentary Research: 242–248.

Eskelinen A, Stark S, Mannisto M. 2009. Links between plant community composition, soil organic matter quality and microbial communities in contrasting tundra habitats. Oecologia, 161: 113-123.

Findlay S. 1995. Importance of surface-subsurface exchange in stream ecosystems: The hyporheic zone. Limnology and Oceanography, 40: 159-164.

Folkard AM. 2011. Vegetated flows in their environmental context: a review. Proceedings of the Institution of Civil Engineers - Engineering and Computational Mechanics, 164: 3-24.

Folkard AM. 2019. Biophysical interactions in fragmented marine canopies: Fundamental processes, consequences, and upscaling. Frontiers in Marine Science, 6: 17.

Forshay KJ, Dodson SI. 2011. Macrophyte presence is an indicator of enhanced denitrification and nitrification in sediments of a temperate restored agricultural stream. Hydrobiologia, 668: 21-34.

Goring DG, Nikora VI. 2002. Despiking acoustic Doppler velocimeter data. Journal of Hydraulic Engineering, 128: 117-126.

Gutiérrez JL, Jones CG. 2006. Physical ecosystem engineers as agents of biogeochemical heterogeneity. Bioscience, 56: 227-236.

Hastings A, Byers JE, Crooks JA, Cuddington K, Jones CG, Lambrinos JG, Talley TS, Wilson WG. 2007. Ecosystem engineering in space and time. Ecology Letters, 10: 153-164.

Hendriks IE, Bouma TJ, Morris EP, Duarte CM. 2009. Effects of seagrasses and algae of the *Caulerpa* family on hydrodynamics and particle-trapping rates. Marine Biology, 157: 473-481.

Jampeetong A, Brix H. 2009. Effects of NH_4^+ concentration on growth, morphology and NH_4^+ uptake kinetics of *Salvinia natans*. Ecological Engineering, 35: 695-702.

Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. Oikos, 69: 373-386.

Jones CG, Lawton JH, Shachak M. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology, 78: 1946-1957.

Jones JI, Collins AL, Naden PS, Sear DA. 2012. The relationship between fine sediment and macrophytes in rivers. River Research and Applications, 28: 1006-1018.

Klausmeier CA. 1999. Regular and irregular patterns in semiarid vegetation. Science, 284: 1826-1828.

Kristensen E, Ahmed SI, Devol AH. 1995. Aerobic and anaerobic decomposition of organic matter in marine sediment: Which is fastest? Limnology and Oceanography, 40: 1430-1437.

Ladd J, Jackson R. 1982. Biochemistry of ammonification. In: Stevenson FJ, editor. Nitrogen in agricultural soils. 22, Madison, USA, pp. 173-228.

Lavorel S, Diaz S, Cornelisen JHC, Garnier E, Harrison SP, McIntyre S, Pausas JG, Perez-Harguindeguy N, Roumet C, Urcelay C. 2007. Plant functional types: Are we getting any closer to the Holy Grail? In: Canadell JG PD, Pitelka L, editor. Terrestrial Ecosystems in a Changing World. Springer-Verlag, Berlin Heidelberg, pp. 149-164.

Lefebvre S, Marmonier P, Pinay G. 2004. Stream regulation and nitrogen dynamics in sediment interstices: Comparison of natural and straightened sectors of a third-order stream. River Research and Applications, 20: 499-512.

Lefebvre S, Marmonier P, Pinay G, Bour O, Aquilina L, Baudry J. 2005. Nutrient dynamics in interstitial habitats of low-order rural streams with different bedrock geology. Archiv für Hydrobiologie, 164: 169-191.

Lemoine DG, Mermillod-Blondin F, Barrat-Segretain M-H, Massé C, Malet E. 2012. The ability of aquatic macrophytes to increase root porosity and radial oxygen loss determines their resistance to sediment anoxia. Aquatic ecology, 46: 191-200.

Licci S, Nepf H, Delolme C, Marmonier P, Bouma TJ, Puijalon S. 2019. The role of patch size in ecosystem engineering capacity: a case study of aquatic vegetation. Aquatic Sciences, 81.

Liu C, Nepf H. 2016. Sediment deposition within and around a finite patch of model vegetation over a range of channel velocity. Water Resources Research, 52: 600-612.

Marjoribanks TI, Hardy RJ, Lane SN, Tancock MJ. 2017. Patch-scale representation of vegetation within hydraulic models. Earth Surface Processes and Landforms, 42: 699-710.

McCave IN, Syvitski JPM. 1991. Principles and methods of geological particle size analysis. In: Syvitski JPM, editor. Principles, Methods and Application of Particle Size Analysis. Cambridge University Press, Cambridge, pp. 3-21.

McClain ME, Boyer EW, Dent CL, Gergel SE, Grimm NB, Groffman PM, Hart SC, Harvey JW, Johnston CA, Mayorga E, McDowell WH, Pinay G. 2003. Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. Ecosystems, 6: 301-312.

Mermillod-Blondin F, Lemoine D, Boisson JC, Malet E, Montuelle B. 2008. Relative influences of submersed macrophytes and bioturbating fauna on biogeochemical processes and microbial activities in freshwater sediments. Freshwater Biology, 53: 1969-1982.

Mori N, Suzuki T, Kakuno S. 2007. Noise of acoustic Doppler velocimeter data in bubbly flows. Journal of engineering mechanics, 133: 122-125.

Morrice JA, Valett H, Dahm CN, Campana ME. 1997. Alluvial characteristics, groundwater–surface water exchange and hydrological retention in headwater streams. Hydrological Processes, 11: 253-267.

Navel S, Mermillod-Blondin F, Montuelle B, Chauvet E, Marmonier P. 2012. Sedimentary context controls the influence of ecosystem engineering by bioturbators on microbial processes in river sediments. OIKOS, 121: 1134-1144.

Nepf HM. 2012. Hydrodynamics of vegetated channels. Journal of Hydraulic Research, 50: 262-279.

Nichols DS, Keeney DR. 1976. Nitrogen nutrition of *Myriophyllum spicatum*: uptake and translocation of 15N by shoots and roots. Freshwater Biology, 6: 145-154.

Nimptsch J, Pflugmacher S. 2007. Ammonia triggers the promotion of oxidative stress in the aquatic macrophyte *Myriophyllum mattogrossense*. Chemosphere, 66: 708-714.

Phillips JM, Walling DE. 1999. The particle size characteristics of fine- grained channel deposits in the River Exe Basin, Devon, UK. Hydrological Processes, 13: 1-19.

Pluntke, T., and H.-P. Kozerski. 2003. Particle trapping on leaves and on the bottom in simulated submerged plant stands. Hydrobiologia 506-509:575-581.

Pretty JL, Hildrew AG, Trimmer M. 2006. Nutrient dynamics in relation to surface-subsurface hydrological exchange in a groundwater fed chalk stream. Journal of Hydrology, 330: 84-100.

Puijalon, S., and G. Bornette. 2004. Morphological variation of two taxonomically distant plant species along a natural flow velocity gradient. New Phytologist 163:651-660.

Puijalon S, Bouma TJ, Douady CJ, van Groenendael J, Anten NPR, Martel E, Bornette G. 2011. Plant resistance to mechanical stress : evidence of an avoidance-tolerance trade-off. New Phytologist, 191: 1141-1149.

Puijalon S, Léna J-P, Bornette G. 2007. Interactive effects of nutrient and mechanical stresses on plant morphology. Annals of Botany, 100: 1297-1305.

Puijalon S, Léna J-P, Rivière N, Champagne J-Y, Rostan J-C, Bornette G. 2008. Phenotypic plasticity in response to mechanical stress: hydrodynamic performance and fitness of 4 aquatic plant species. New Phytologist, 177: 907-917.

Quade D. 1979. Using Weighted Rankings in the Analysis of Complete Blocks with Additive Block Effects. Journal of the American Statistical Association, 74: 680-683.

Reitsema RE, Preiner S, Meire P, Hein T, Dai YR, Schoelynck J. 2021. Environmental control of macrophyte traits and interactions with metabolism and hydromorphology in a groundwater-fed river. River Research and Applications, 37: 294-306.

Rietkerk M, van de Koppel J. 2008. Regular pattern formation in real ecosystems. Trends in Ecology & Evolution, 23: 169-175.

Rudolph H, Voigt JU. 1986. Effects of NH_4^+- N and NO_3^-- N on growth and metabolism of *Sphagnum magellanicum*. Physiologia plantarum, 66: 339-343.

Sand-Jensen K. 1998. Influence of submerged macrophytes on sediment composition and near-bed flow in lowland streams. Freshwater Biology, 39: 663-679.

Sand-Jensen K, Binzer T, Middelboe AL. 2007. Scaling of photosynthetic production of aquatic macrophytes - a review. OIKOS, 116: 280-294.

Sand-Jensen K, Madsen TV. 1992. Patch dynamics of the stream macrophyte, *Callitriche cophocarpa*. Freshwater Biology, 27: 277-282.

Sand-Jensen K, Mebus JR. 1996. Fine-scale patterns of water velocity within macrophyte patches in streams. Oikos, 76: 169-180.

Sand-Jensen K, Pedersen ML. 2008. Streamlining of plant patches in streams. Freshwater Biology, 53: 714-726.

Sand-Jensen K, Prahl C, Stokholm H. 1982. Oxygen release from roots of submerged aquatic macrophytes. Oikos, 38: 349.

Sand- Jensen K, Borum J, Binzer T. 2005. Oxygen stress and reduced growth of *Lobelia dortmanna* in sandy lake sediments subject to organic enrichment. Freshwater Biology, 50: 1034-1048.

Sanders I, Heppell C, Cotton J, Wharton G, Hildrew A, Flowers E, Trimmer M. 2007. Emission of methane from chalk streams has potential implications for agricultural practices. Freshwater Biology, 52: 1176-1186.

Sanders IA, Trimmer M. 2006. In situ application of the $^{15}NO_3^-$ isotope pairing technique to measure denitrification in sediments at the surface water- groundwater interface. Limnology and Oceanography: Methods, 4: 142-152.

Schneider S, Melzer A. 2004. Sediment and water nutrient characteristics in patches of submerged macrophytes in running waters. Hydrobiologia, 527: 195-207.

Schoelynck J, Bal K, Verschoren V, Penning E, Struyf E, Bouma T, Meire D, Meire P, Temmerman S. 2014. Different morphology of *Nuphar lutea* in two contrasting aquatic environments and its effect on ecosystem engineering. Earth Surface Processes and Landforms, 39: 2100-2108.

Schoelynck J, de Groote T, Bal K, Vandenbruwaene W, Meire P, Temmerman S. 2012. Self-organised patchiness and scale-dependent bio-geomorphic feedbacks in aquatic river vegetation. Ecography, 35: 760-768.

Schoelynck J, Meire D, Bal K, Buis K, Troch P, Bouma T, Meire P, Temmerman S. 2013. Submerged macrophytes avoiding a negative feedback in reaction to hydrodynamic stress. Limnologica - Ecology and Management of Inland Waters, 43: 371-380.

Schoelynck J, Schaller J, Murray-Hudson M, Frings PJ, Conley DJ, van Pelt D, Mosimane K, Gondwe M, Wolski P, Meire P, Struyf E. 2017. The trapping of organic matter within plant patches in the channels of the Okavango Delta: a matter of quality. Aquatic Sciences, 79: 661-674.

Schulz M, Kozerski HP, Pluntke T, Rinke K. 2003. The influence of macrophytes on sedimentation and nutrient retention in the lower River Spree (Germany). Water Research, 37: 569-578.

Seitzinger SP. 1988. Denitrification in freshwater and coastal marine ecosystems: ecological and geochemical significance. Limnology and Oceanography, 33: 702-724.

Shelley F, Klaar M, Krause S, Trimmer M. 2017. Enhanced hyporheic exchange flow around woody debris does not increase nitrate reduction in a sandy streambed. Biogeochemistry, 136: 353-372.

Soana E, Bartoli M. 2013. Seasonal variation of radial oxygen loss in *Vallisneria spiralis* L.: An adaptive response to sediment redox? Aquatic Botany, 104: 228-232.

Su HJ, Chen J, Wu Y, Chen JF, Guo XC, Yan ZB, Tian D, Fang JY, Xie P. 2019. Morphological traits of submerged macrophytes reveal specific positive feedbacks to water clarity in freshwater ecosystems. Science of the Total Environment, 684: 578-586.

Su S, Yiming Z, Jian Q, Wang W, Yao W, Song L. 2012. Physiological responses of *Egeria densa* to high ammonium concentration and nitrogen deficiency. Chemosphere, 86: 538-545.

Sukhodolov AN, Sukhodolova TA. 2010. Case study: effect of submerged aquatic plants on turbulence structure in a lowland river. Journal of Hydraulic Engineering, 136: 434-446.

Teles V, Bravard JP, De Marsily G, Perrier E. 2001. Modelling of the construction of the Rhone alluvial plain since 15 000 years BP. Sedimentology, 48: 1209-1224.

Tison J-M, de Foucault B. 2014s. Flora Gallica - Flore de France.

Trimmer M, Sanders IA, Heppell CM. 2009. Carbon and nitrogen cycling in a vegetated lowland chalk river impacted by sediment. Hydrological Processes, 23: 2225-2238.

van de Koppel J, Crain CM. 2006. Scale-dependent inhibition drives regular tussock spacing in a freshwater marsh. The American Naturalist, 168: E136-E147.

Vandenbruwaene W, Temmerman S, Bouma TJ, Klaassen PC, de Vries MB, Callaghan DP, van Steeg P, Dekker F, van Duren LA, Martini E, Balke T, Biermans G, Schoelynck J, Meire P. 2011. Flow interaction with dynamic vegetation patches: Implications for biogeomorphic evolution of a tidal landscape. Journal of Geophysical Research-Earth Surface, 116: 1-13.

Verstraete W, Focht DD. 1977. Biochemical ecology of nitrification and denitrification. In: Alexander M, editor. Advances in Microbial Ecology. Springer US, Boston, MA, pp. 135-214.

Wentworth CK. 1922. A scale of grade and class terms for clastic sediments. The Journal of Geology, 30: 377-392.

Wharton G, Cotton JA, Wotton RS, Bass JAB, Heppell CM, Trimmer M, Sanders IA, Warren LL. 2006. Macrophytes and suspension-feeding invertebrates modify flows and fine sediments in the Frome and Piddle catchments, Dorset (UK). Journal of Hydrology, 330: 171-184.

Wigand C, Finn M, Findlay S, Fischer D. 2001. Submersed macrophyte effects on nutrient exchanges in riverine sediments. Estuaries, 24: 398-406.

Xie Y, An S, Yao X, Xiao K, Zhang C. 2005. Short-time response in root morphology of *Vallisneria natans* to sediment type and water-column nutrient. Aquatic Botany, 81: 85-96.

Yu Q, Wang HZ, Li Y, Shao JC, Liang XM, Jeppesen E, Wang HJ. 2015. Effects of high nitrogen concentrations on the growth of submersed macrophytes at moderate phosphorus concentrations. Water Research, 83: 385-395.

Zong LJ, Nepf H. 2010. Flow and deposition in and around a finite patch of vegetation. Geomorphology, 116: 363-372.

Zong LJ, Nepf H. 2011. Spatial distribution of deposition within a patch of vegetation. Water Resources Research, 47.

Figure legends

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

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

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

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

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

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

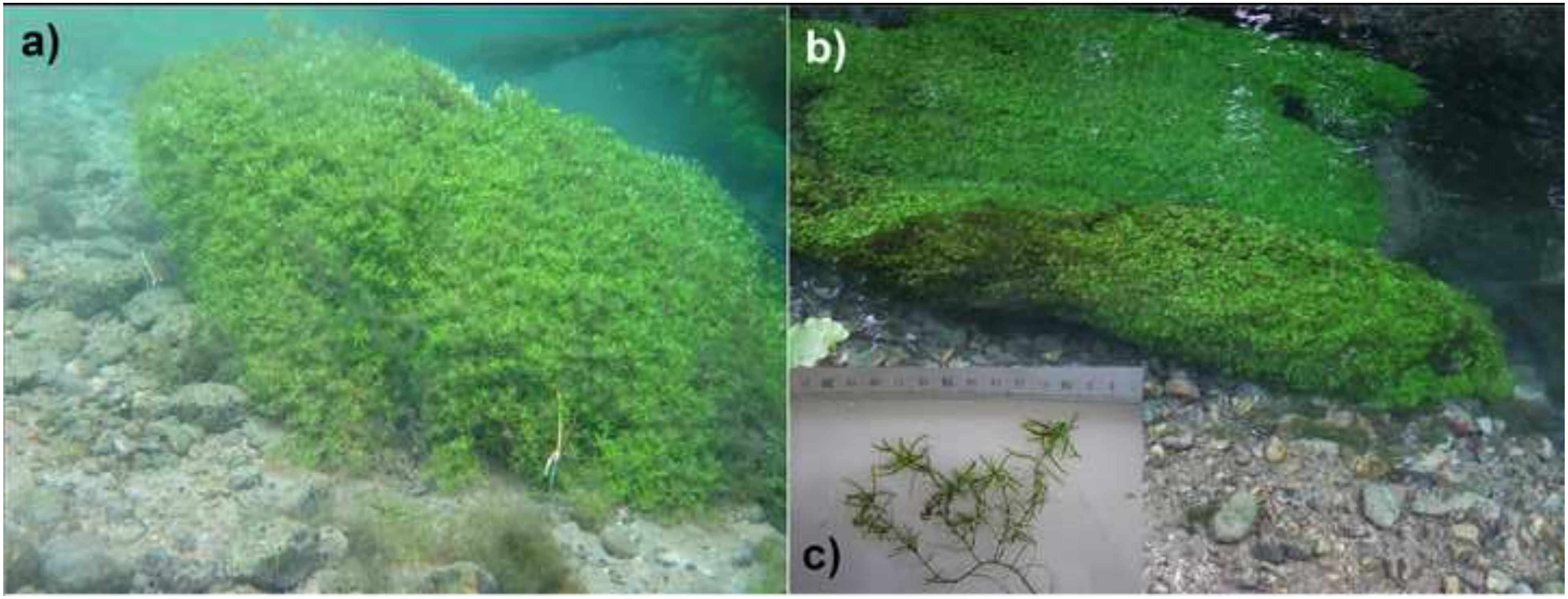
Figure 5. Microbial respiration rate along a short patch (L = 0.3 to 0.33 m) and a long patch (L = 2.27 to 2.50 m) for the two sites, BC and SB. Circles for BC and squares for SB represent the mean value, while error bars represent the standard deviation of the microbial respiration rate for subsamples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

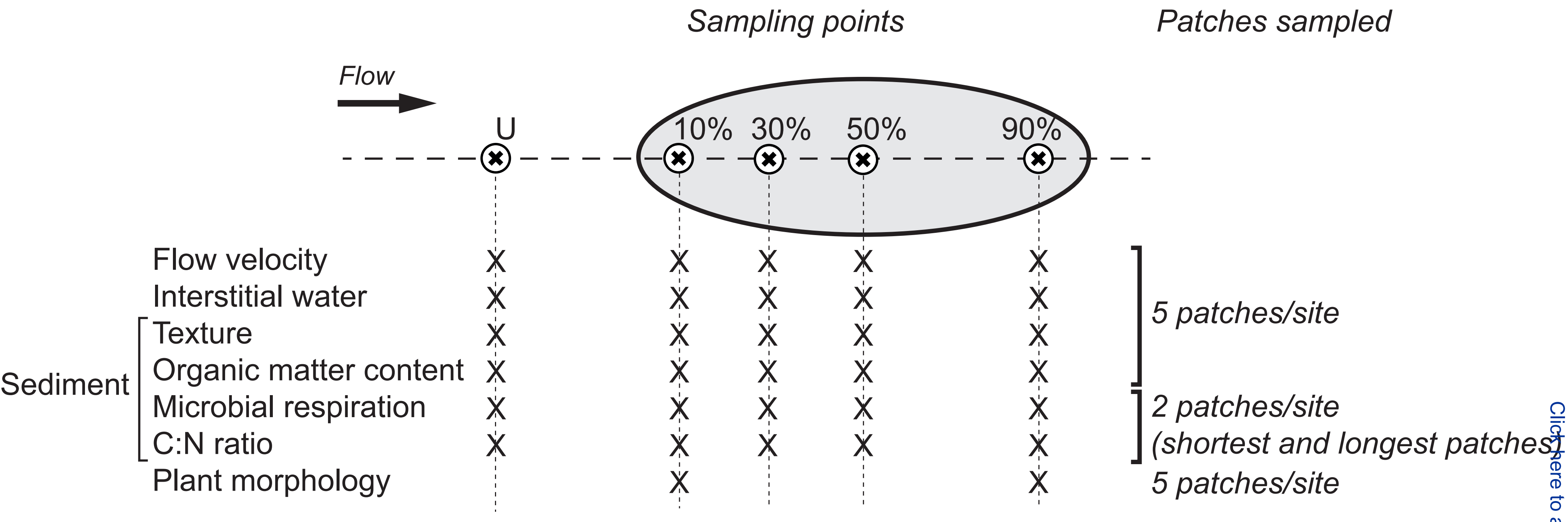
Figure 6. Effect of patch length (L) and position (10% and 90%) on plant height (H_{plant}), along patches of *Callitriche platycarpa*, for site BC at the 10% (a) and 90% (b) positions and for site SB at the 10% (c) and 90% (d) positions. Sampling positions are explained in Figure 2. Circles for BC and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

Tables

Table 1. Comparison of C:N (mean and SD) of sediment in bare sediment and in vegetated sediment for patches of different lengths (Welch t test).

Site	**BC**				**SB**			
Patch length L (m)	**0.33**		**2.27**		**0.30**		**2.50**	
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	


a)
b)
c)


Sampling points
Patches sampled
Flow
U
10%
30%
50%
90%
Flow velocity
Interstitial water
Sediment
Texture
Organic matter content
Microbial respiration
C:N ratio
Plant morphology
5 patches/site
2 patches/site
(shortest and longest patches)
5 patches/site

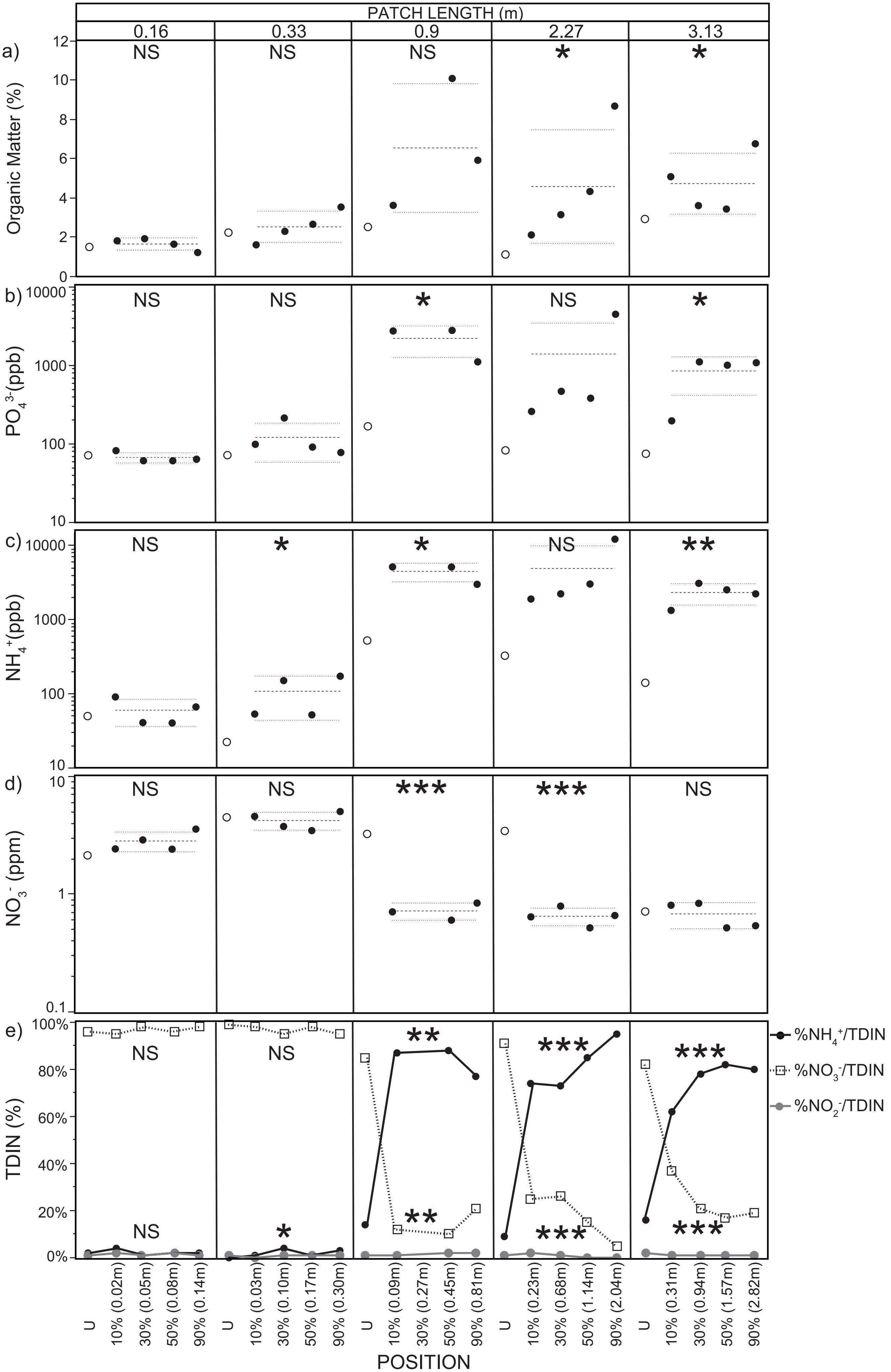

PATCH LENGTH (m)
0.16
0.33
0.9
2.27
3.13
a)
Organic Matter (%)
0
2
4
6
8
10
12
NS
NS
NS
*
*
b)
PO$_4^{3-}$(ppb)
10
100
1000
10000
NS
NS
*
NS
*
c)
NH$_4^+$(ppb)
10
100
1000
10000
NS
*
*
NS
**
d)
NO$_3^-$ (ppm)
0.1
1
10
NS
NS
***
***
NS
e)
TDIN (%)
0%
20%
40%
60%
80%
100%
NS
NS
**
***
***
NS
*
**
***
***
%NH$_4^+$/TDIN
%NO$_3^-$/TDIN
%NO$_2^-$/TDIN
U
10% (0.02m)
30% (0.05m)
50% (0.08m)
90% (0.14m)
U
10% (0.03m)
30% (0.10m)
50% (0.17m)
90% (0.30m)
U
10% (0.09m)
30% (0.27m)
50% (0.45m)
90% (0.81m)
U
10% (0.23m)
30% (0.68m)
50% (1.14m)
90% (2.04m)
U
10% (0.31m)
30% (0.94m)
50% (1.57m)
90% (2.82m)
POSITION

Figure4

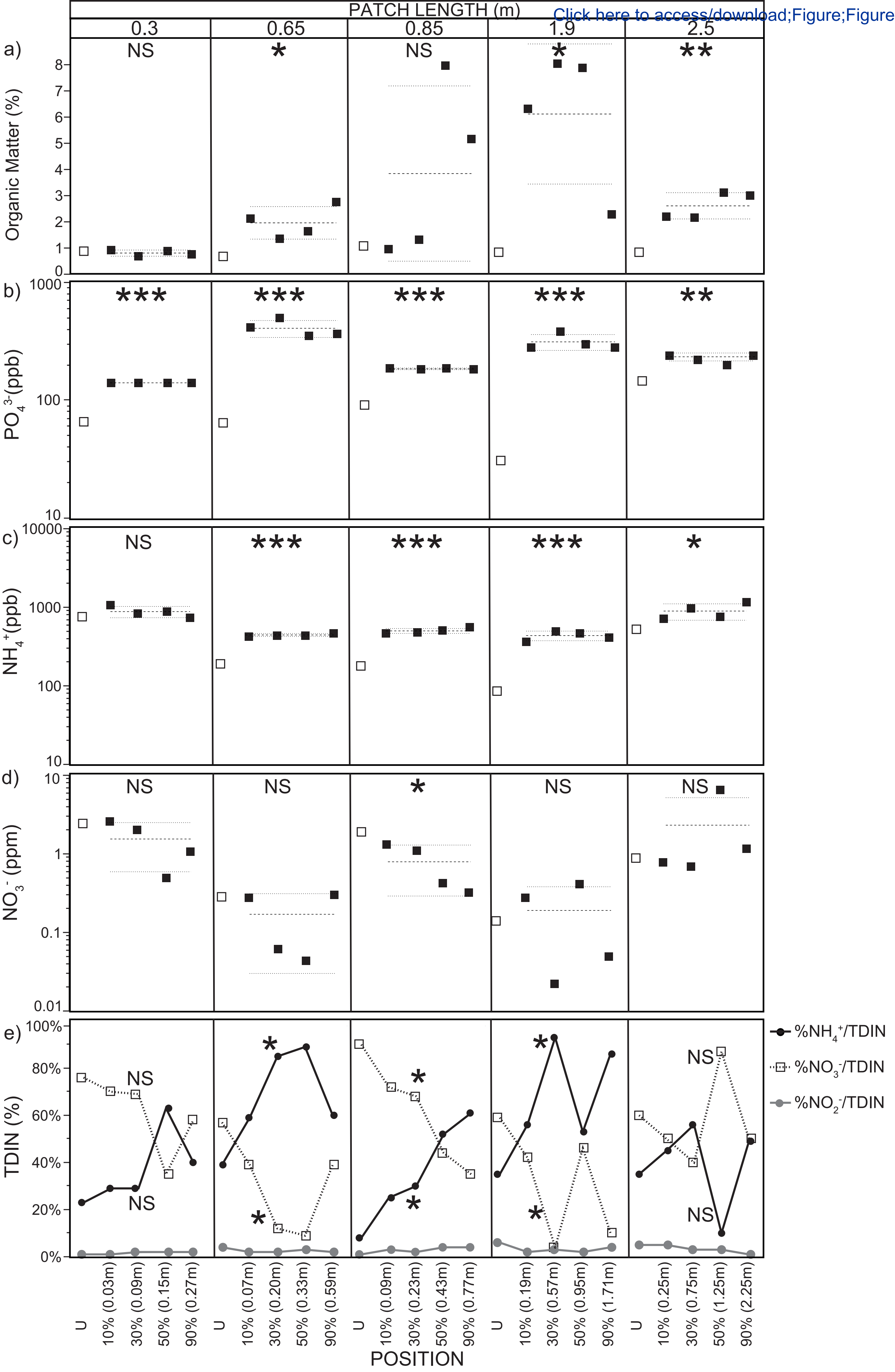

PATCH LENGTH (m)
0.3
0.65
0.85
1.9
2.5
a)
Organic Matter (%)
0
1
2
3
4
5
6
7
8
NS
*
NS
*
**
b)
PO_4^{3-}(ppb)
10
100
1000
***
***
***
***
**
c)
NH_4^+(ppb)
10
100
1000
10000
NS
***
***
***
*
d)
NO_3^- (ppm)
0.01
0.1
1
10
NS
NS
*
NS
NS
e)
TDIN (%)
0%
20%
40%
60%
80%
100%
NS
NS
*
*
*
*
*
*
NS
NS
%NH_4^+/TDIN
%NO_3^-/TDIN
%NO_2^-/TDIN
U
10% (0.03m)
30% (0.09m)
50% (0.15m)
90% (0.27m)
U
10% (0.07m)
30% (0.20m)
50% (0.33m)
90% (0.59m)
U
10% (0.09m)
30% (0.23m)
50% (0.43m)
90% (0.77m)
U
10% (0.19m)
30% (0.57m)
50% (0.95m)
90% (1.71m)
U
10% (0.25m)
30% (0.75m)
50% (1.25m)
90% (2.25m)
POSITION

Figure5

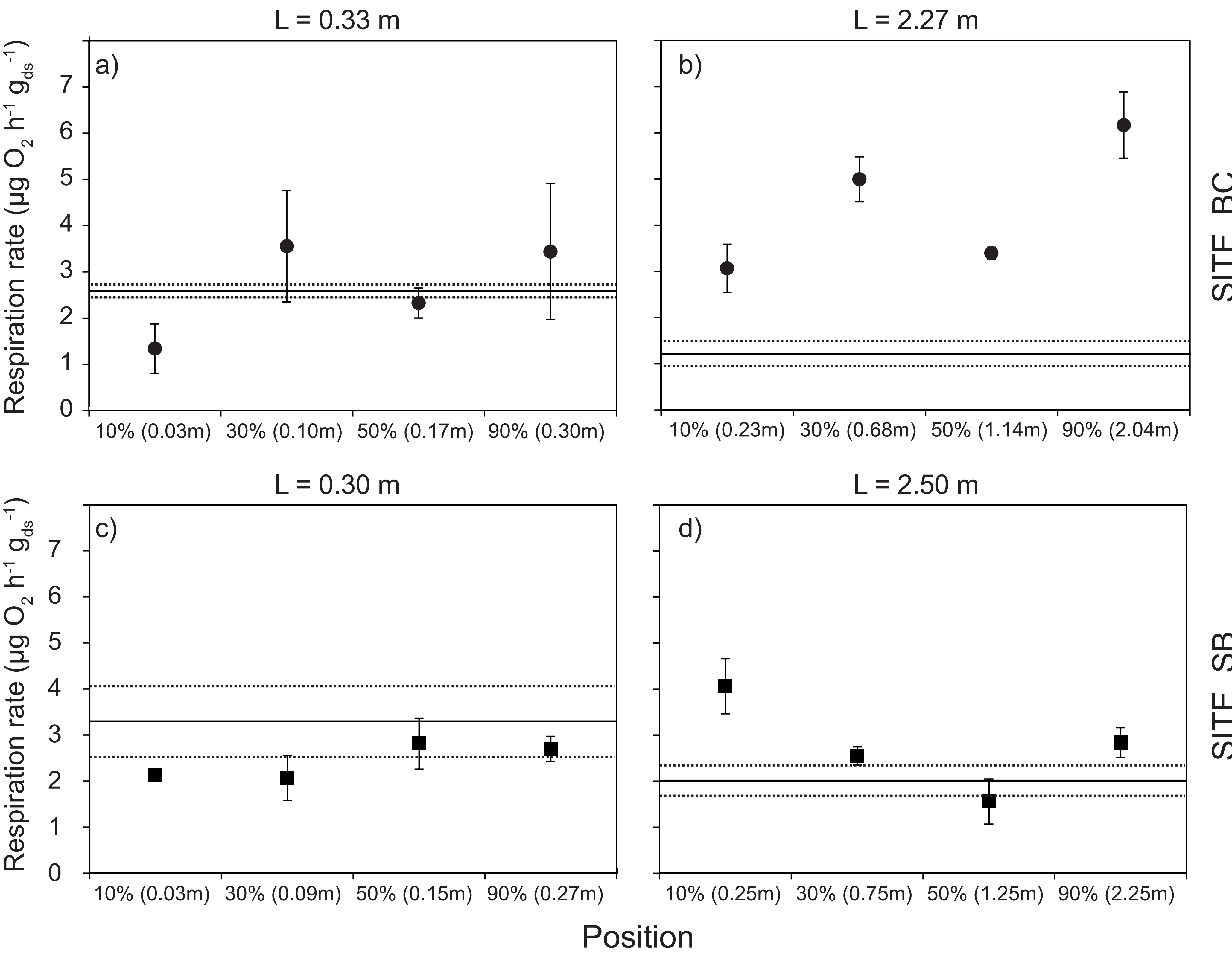
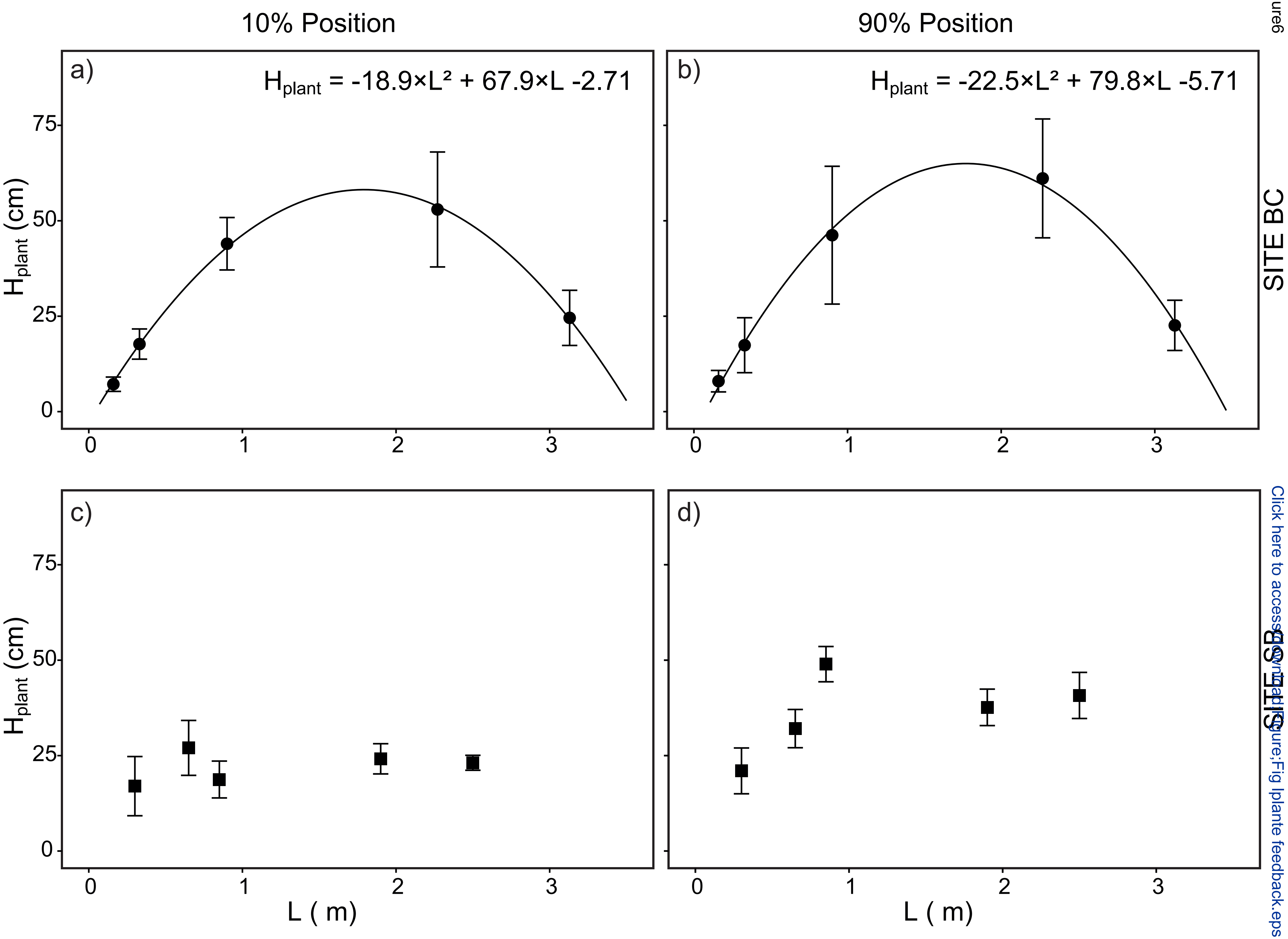

L = 0.33 m
L = 2.27 m
SITE BC
a)
b)
Respiration rate (µg O_2 h^{-1} g_{ds}^{-1})
7
6
5
4
3
2
1
0
10% (0.03m)
30% (0.10m)
50% (0.17m)
90% (0.30m)
10% (0.23m)
30% (0.68m)
50% (1.14m)
90% (2.04m)
L = 0.30 m
L = 2.50 m
SITE SB
c)
d)
Respiration rate (µg O_2 h^{-1} g_{ds}^{-1})
10% (0.03m)
30% (0.09m)
50% (0.15m)
90% (0.27m)
10% (0.25m)
30% (0.75m)
50% (1.25m)
90% (2.25m)
Position

Figure6


10% Position
90% Position
SITE BC
SITE SB
a)
b)
c)
d)
H_{plant} = -18.9×L² + 67.9×L -2.71
H_{plant} = -22.5×L² + 79.8×L -5.71
H_{plant} (cm)
0
25
50
75
L (m)
0
1
2
3

Supplementary Information

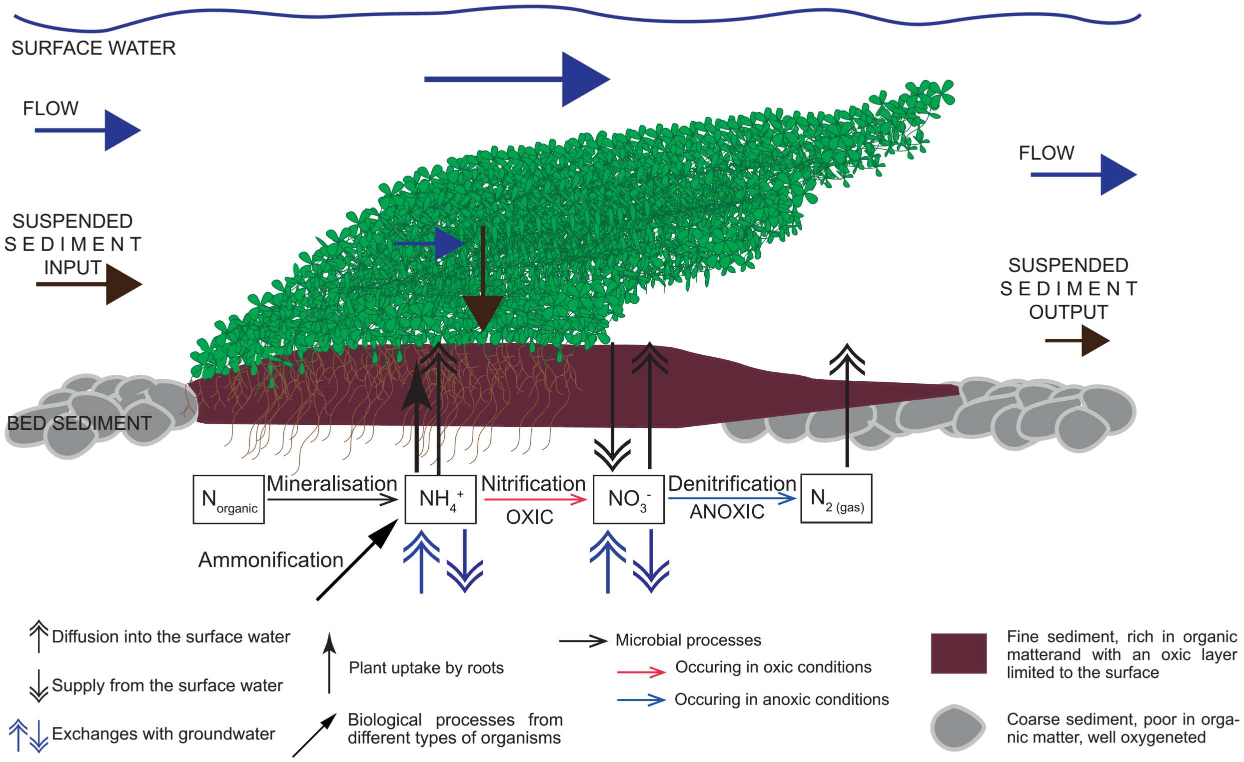


Fig. S1. Processes regulating the ammonium concentrations in interstitial water under patches of aquatic plants in rivers. The ammonium concentrations in the sediment are controlled firstly by the accumulation of fine sediment and organic material, promoted by the deceleration of flow within plant patches (Sand-Jensen, 1998; Cotton et al., 2005). As fine sediment presents a reduced surface-subsurface water exchange, it is less oxygenated compared to the bare sediment, which is coarser (Findlay, 1995; Morrice et al., 1997). Organic matter contains organic nitrogen that is transformed by bacteria into ammonium by mineralisation. In addition, all organisms produce and release ammonia by ammonification (Ladd and Jackson, 1982). Under oxic conditions ammonium is transformed in nitrates through nitrification, this process is limited to the sediment surface in the case of limitation of water exchanges due to fine sediment (Verstraete and Focht, 1977; Schmidt, 1982). Certain aquatic plants are able to release oxygen by root increasing the oxygen availability for nitrifying bacteria, also in deeper sediment (Armstrong, 1971; Lemoine et al., 2012). Under anoxic conditions denitrifying bacteria can transform nitrates in diatomic nitrogen, reducing the nitrogen availability for the system (Verstraete and Focht, 1977; Seitzinger, 1988). Ammonium is the predominant source of nitrogen for aquatic plants, which is followed by nitrates. Due to the higher concentrations of ammonium in the interstitial water compared to the surface water, plants uptake more easily ammonium by roots (Barko and Smart, 1986; Barko et al., 1991). However, high concentrations of ammonium can be toxic for plants (Britto and Kronzucker, 2002; Nimptsch and Pflugmacher, 2007). For this reason, the biogeochemical processes regulating the ammonium concentrations in interstitial water are fundamental for plant growth and survival in rivers.

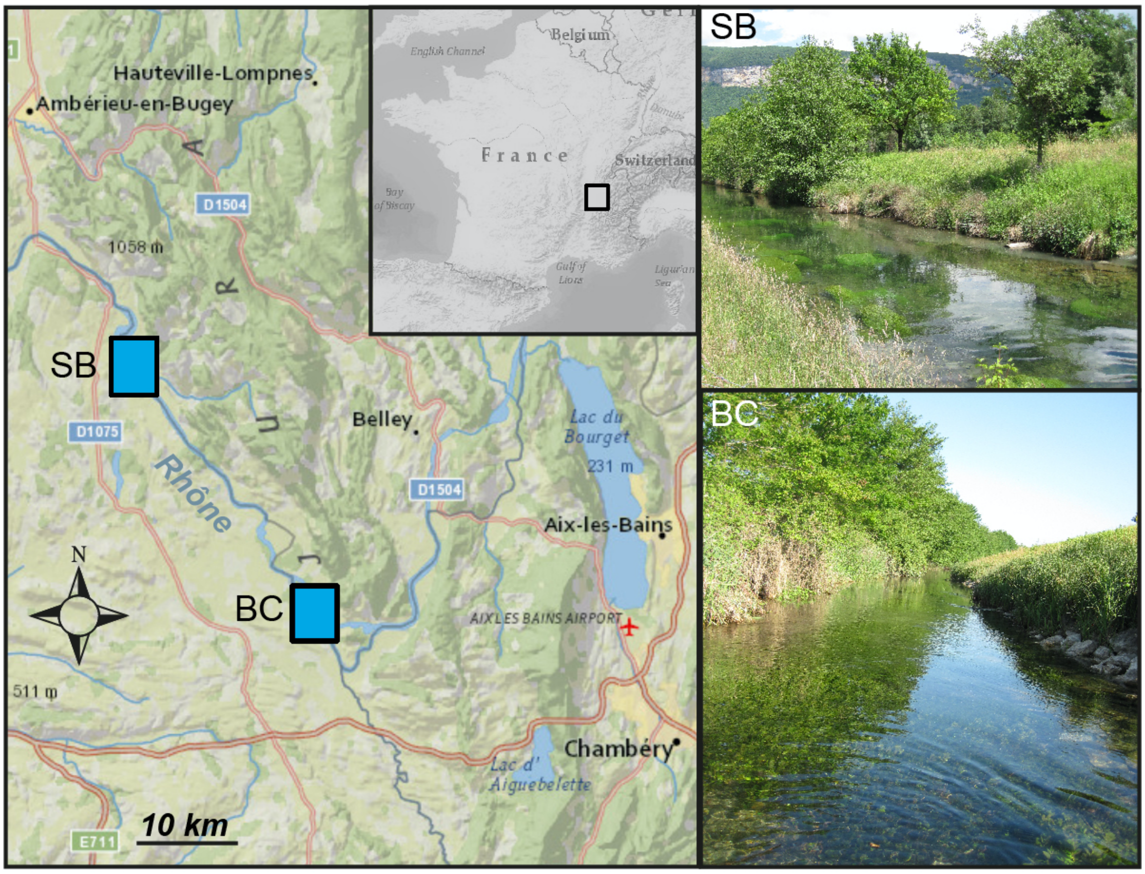


Figure S2. Location and view of the two sites along the Rhône River, France (SB: Serrières-de-Briord; BC: Brégnier-Cordon).

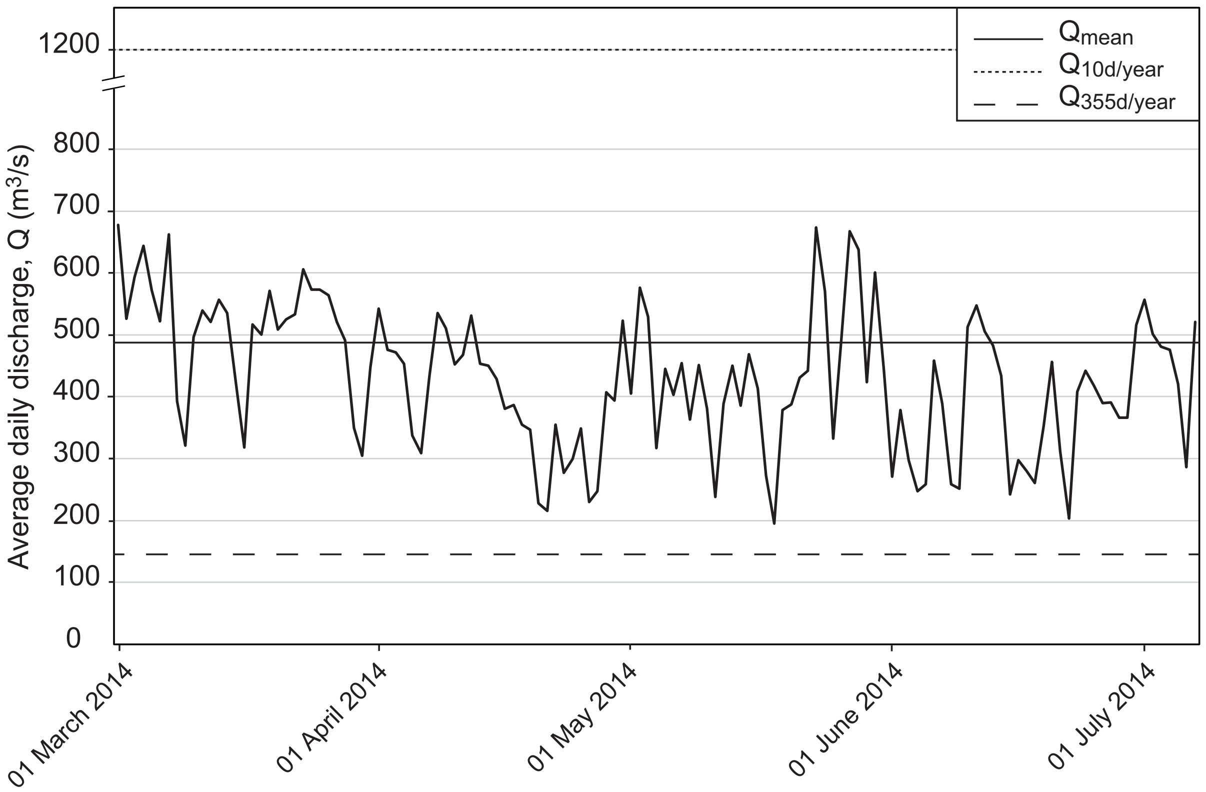


Figure S3. Hydrograph for the period between March and July 2014 for the Rhône River, at Lagnieu (average daily discharge, m^3/s). The lines represent the average discharge (Q_{mean}, black line), the average daily discharge exceeded 10 days/year ($Q_{10d/year}$, dotted line) and the average daily discharge exceeded 355 days/year ($Q_{355d/year}$, dashed line). Data from HYDRO bank (https://www.hydro.eaufrance.fr/).

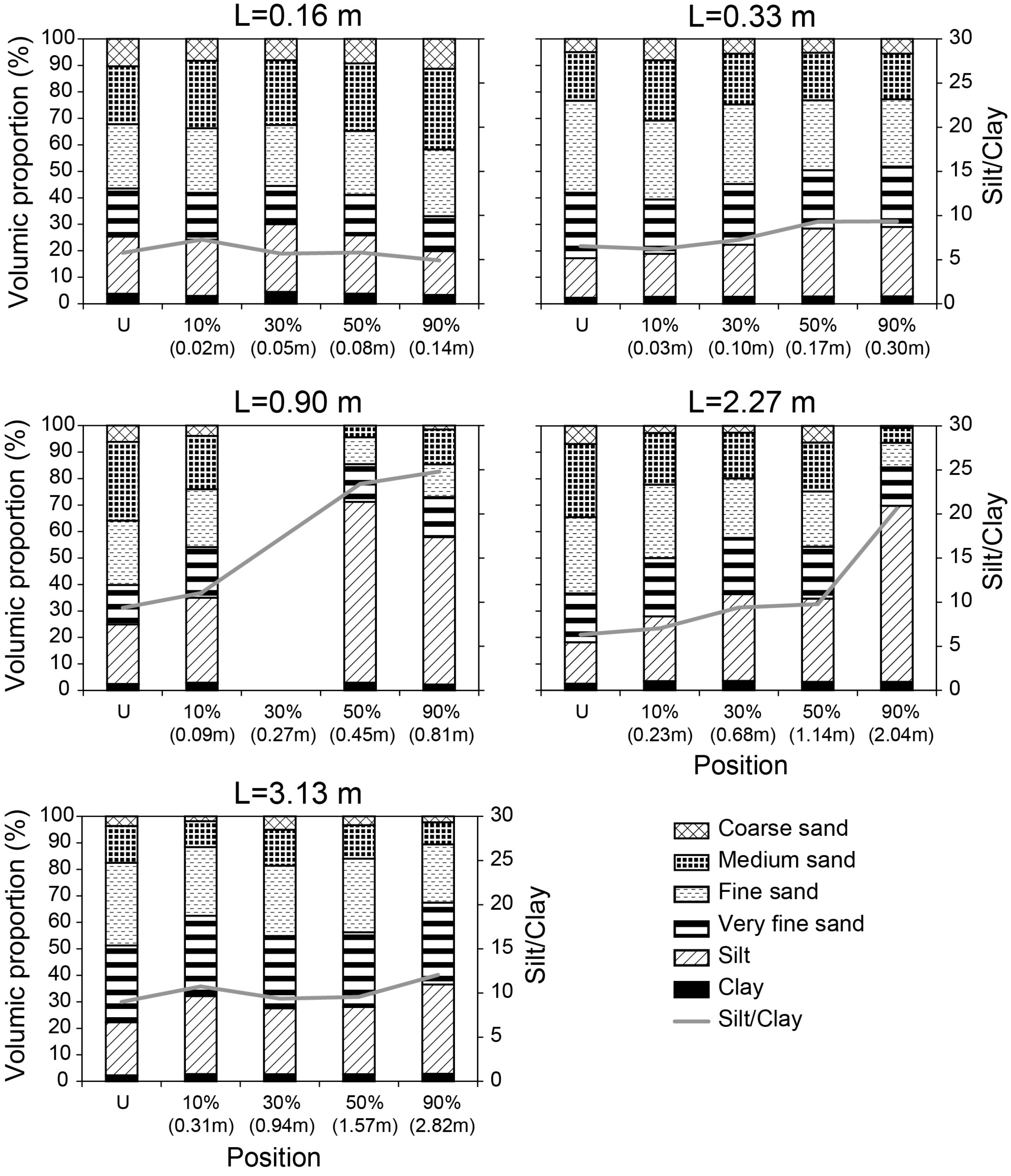


Figure S4. Sediment grain size distributions and silt to clay ratio at the sampling positions of the patches of increasing length of *C. platycarpa* at the site BC. Sediment classification follows the Wentworth size classes (Wentworth, 1922).

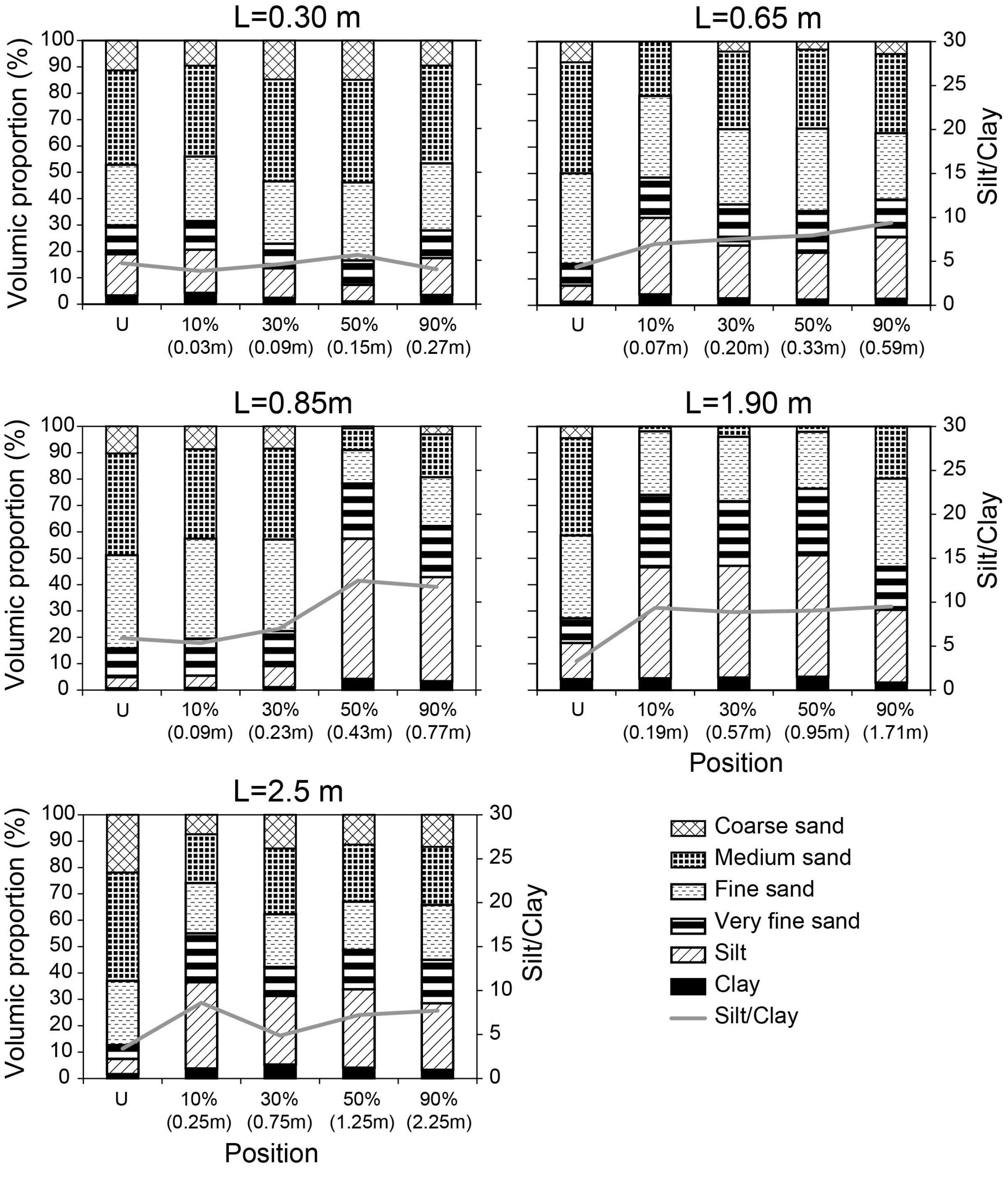


Figure S5. Sediment grain size distributions and silt to clay ratio at the sampling positions of the patches of increasing length of *C. platycarpa* at the site SB. Sediment classification follows the Wentworth size classes (Wentworth, 1922).

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

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

		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
Surface water characteristics	**Λ (µS cm^{-1})**	373.1 ± 3.7	443.4 ± 5.0	t_8 = 25.3 ; $p<10^{-4}$
	T(°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
	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	**PO_4^{3-} (ppb)**	94.0 ± 41.6	79.3 ± 42.3	t_8 = -0.55 ; p=0.60
	NH_4^+ (ppb)	213.3 ± 211.3	346.8 ± 284.2	t_8 = 0.84 ; p=0.42
	NO_3^- (ppm)	2.81± 1.44	1.13 ± 1.02	t_8 = -2.12 ; p=0.07
	NO_2^- (ppb)	33.4 ± 12.9	32.8 ± 27.6	t_8 = -0.05 ; p=0.96

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

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

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

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

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

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 Matter	t_3	0.95	0.72	2.13	2.39	02.32	-1.17	4.10	1.66	3.97	7.11
	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^+/ TDIN	t_3	-0.35	2.93	19.9	14.2	12.5	2.09	4.35	3.91	3.54	0.51
	p	0.62	0.03	0.001	$<10^{-3}$	$<10^{-3}$	0.06	0.011	0.015	0.019	0.32
%NO_3^- /TDIN	t_3	0.07	-2.27	-20.2	-14.9	-12.7	-2.17	-3.96	-3.93	-3.10	-0.29
	p	0.52	0.054	0.001	$<10^{-3}$	$<10^{-3}$	0.06	0.014	0.015	0.027	0.40

References

Armstrong W. 1971. Radial oxygen losses from intact rice roots as affected by distance from the apex, respiration and waterlogging. Physiologia plantarum, 25: 192-197.

Barko JW, Gunnison D, Carpenter SR. 1991. Sediment interactions with submersed macrophyte growth and community dynamics. Aquatic Botany, 41: 41-65.

Barko JW, Smart RM. 1986. Sediment-related mechanisms of growth limitation in submersed macrophytes. Ecology, 67: 1328-1340.

Britto DT, Kronzucker HJ. 2002. NH_4^+ toxicity in higher plants: a critical review. Journal of Plant Physiology, 159: 567-584.

Cotton JA, Heppell CM, Wharton G, Bass JA. 2005. In-channel storage of fine sediment in vegetated rivers: implications for catchment sediment budgets. Materials and Geoenvironment, 52: 200.

Findlay S. 1995. Importance of surface-subsurface exchange in stream ecosystems: The hyporheic zone. Limnology and Oceanography, 40: 159-164.

Ladd J, Jackson R. 1982. Biochemistry of ammonification. In: Stevenson FJ, editor. Nitrogen in agricultural soils. 22, Madison, USA, pp. 173-228.

Lemoine DG, Mermillod-Blondin F, Barrat-Segretain M-H, Massé C, Malet E. 2012. The ability of aquatic macrophytes to increase root porosity and radial oxygen loss determines their resistance to sediment anoxia. Aquatic ecology, 46: 191-200.

Morrice JA, Valett H, Dahm CN, Campana ME. 1997. Alluvial characteristics, groundwater–surface water exchange and hydrological retention in headwater streams. Hydrological Processes, 11: 253-267.

Nimptsch J, Pflugmacher S. 2007. Ammonia triggers the promotion of oxidative stress in the aquatic macrophyte *Myriophyllum mattogrossense*. Chemosphere, 66: 708-714.

Sand-Jensen K. 1998. Influence of submerged macrophytes on sediment composition and near-bed flow in lowland streams. Freshwater Biology, 39: 663-679.

Schmidt EL. 1982. Nitrification in soil. In: FJ S, editor. Nitrogen in agricultural soils. 22, Madison, USA, pp. 253-288.

Seitzinger SP. 1988. Denitrification in freshwater and coastal marine ecosystems: ecological and geochemical significance. Limnology and Oceanography, 33: 702-724.

Verstraete W, Focht DD. 1977. Biochemical ecology of nitrification and denitrification. In: Alexander M, editor. Advances in Microbial Ecology. Springer US, Boston, MA, pp. 135-214.

Wentworth CK. 1922. A scale of grade and class terms for clastic sediments. The Journal of Geology, 30: 377-392.