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**Physical habitat modifications
by submerged aquatic vegetation:
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Physical habitat modifications by submerged aquatic vegetation: consequences for biogeochemical processes and feedbacks for plants

Abstract

Submerged aquatic vegetation often grows in lotic systems in patches generated by scale-dependent feedbacks. As ecosystem engineers, plants modify the physical environment triggering positive feedbacks within the patch and negative feedbacks alongside the patch, resulting in regular pattern formation. These scale-dependent feedbacks enable to explain only the lateral expansion of patches, but not their longitudinal development. The objective was to study the processes that trigger positive and negative feedbacks for plants along patches and the consequences for patch dynamics. In situ coupled measurements of hydrodynamics, sediment characteristics, and plant morphology were performed along patches of increasing length. The results demonstrated that a minimum patch length was needed to induce in-patch velocity reduction and fine sediment accumulation. As a consequence of these modifications, patch length influenced the nutrient concentrations in interstitial water of the in-patch sediment, this effect being observed only over a certain threshold length. Over this threshold length, the sediment presented an accumulation of ammonium and depletion of nitrates. Plant height was related to patch length by a quadratic relationship, suggesting that negative feedbacks occur over a certain patch length, probably due to the high ammonium concentration that can be toxic for plants in the range measured. The threshold lengths over which patches influence the biogeochemical processes and negative feedbacks occur were reduced in the ecosystem presenting the highest nutrient level. The results also demonstrated that the physical habitat modifications induced by patches depend on the plant traits and patch characteristics. The plant-induced modifications of the physical habitat have cascading effects on the biogeochemical processes and plant growth, which depended on the environmental conditions, with consequences for patch dynamics and ecosystem functioning.

Keywords: hydrodynamics, sediment, biogeochemical processes, ecosystem engineering, scale-dependent feedbacks, submerged aquatic vegetation, traits, patch dynamics.

Modifications physiques de l'habitat par les végétaux aquatiques : conséquences pour les processus biogéochimiques et rétroactions pour les plantes

Résumé

Dans les systèmes lotiques, la végétation aquatique se développe en formant des taches générées par des rétroactions échelle-dépendantes. Les plantes modifient l'environnement physique (i.e. organismes ingénieurs), induisant des rétroactions positives dans les taches et négatives à côté, ce qui conduit à la formation de patrons réguliers. Ces rétroactions échelle-dépendantes ne permettent d'expliquer que l'expansion latérale des taches, mais pas leur développement longitudinal. L'objectif était d'étudier les processus qui induisent des rétroactions pour les plantes et les conséquences pour la dynamique des taches. Des mesures de l'hydrodynamique, des caractéristiques des sédiments et de la morphologie des plantes ont été faites in situ le long de taches de longueur croissante. Les résultats ont démontré qu'une longueur minimale est nécessaire pour induire une réduction de la vitesse du courant et une accumulation de sédiments fins dans les taches. L'ensemble conduit à des changements des concentrations en nutriments dans l'eau interstitielle au delà d'une certaine longueur de tache, consistant en une accumulation d'ammonium et une diminution des nitrates. La hauteur des plantes est liée à la longueur de la tache selon un modèle quadratique, suggérant l'existence d'une rétroaction négative au delà d'une longueur seuil, probablement due à la concentration élevée en ammonium qui peut être toxique pour les plantes. Les longueurs au delà desquelles ont lieu des changements des processus biogéochimiques et des rétroactions négatives sont plus faibles dans l'écosystème avec le niveau de nutriments le plus élevé. Enfin, les modifications de l'habitat induites par les taches dépendent des caractéristiques des plantes et des taches. Ces modifications induites par les plantes ont des effets en cascade sur les processus biogéochimiques et la croissance des plantes, avec des conséquences pour la dynamique des taches et le fonctionnement de l'écosystème.

Mots clés : Hydrodynamique, sédiment, processus biogéochimiques, organisme ingénieur, rétroactions échelle-dépendantes, végétation aquatique submergée, traits, dynamique des taches.

Résumé substantiel

L'étude de la formation et de la dynamique des patrons réguliers est l'un des sujets majeurs de l'écologie. Les patrons réguliers de la végétation peuvent être causés par l'hétérogénéité de l'environnement, mais ils peuvent aussi être observés dans des conditions environnementales homogènes. La formation de patrons réguliers dans des conditions environnementales homogènes, appelée auto-organisation spatiale, peut résulter d'interactions entre les organismes et l'environnement se produisant à différentes échelles. De tels patrons sont fréquemment observés dans des environnements stressants. Les organismes ingénieurs interagissent avec l'environnement en modifiant physiquement les caractéristiques abiotiques de l'environnement et en induisant des rétroactions pour eux-mêmes ou pour d'autres espèces. Lorsque les rétroactions se produisent à différentes échelles, positives à courte distance et négatives à longue distance (rétroactions échelle-dépendants), ces interactions entre les organismes ingénieurs et leur environnement peuvent conduire à des patrons d'auto-organisation spatiale. Les processus conduisant à la formation des patrons réguliers (rétroactions échelle-dépendants) n'ont été reconnus que récemment pour la végétation aquatique submergée dans les systèmes lotiques, même si la formation de taches de végétation dans ces systèmes était déjà documentée depuis longtemps.

La croissance et le développement des taches de plantes aquatiques dans les écosystèmes lotiques sont fortement influencés par l'écoulement, les caractéristiques des sédiments et la disponibilité en nutriments. Les écosystèmes lotiques sont considérés comme des environnements stressants principalement en raison de l'écoulement unidirectionnel qui induit une traînée permanente sur les plantes, pouvant conduire à des ruptures mécaniques de la végétation (brisure de l'appareil végétatif, déracinement). Dans les systèmes lotiques, des stratégies observées à l'échelle de l'individu (par exemple, flexibilité des tiges et des feuilles) et des taches (densité, forme) permettent aux plantes aquatiques de tolérer les forces hydrodynamiques et de se maintenir dans ces systèmes. Les caractéristiques des sédiments contrôlent l'enracinement et l'établissement de la végétation aquatique et influencent la disponibilité des nutriments et de l'oxygène pour les organes souterrains, à travers le contrôle des échanges d'eau interstitielle avec les eaux de surface. Les sédiments fins, comme les sédiments enrichis en limon et en argile, sont moins perméables, moins oxygénés et plus riches en matière organique et en nutriments que les sédiments plus grossiers. De leur côté, la disponibilité en matière organique et en nutriments influence la croissance des plantes. La matière organique et les nutriments, comme les phosphates et l'ammonium, sont généralement

bénéfiques pour la croissance des plantes, jusqu'à un certain seuil au delà duquel la matière organique peut entraîner l'accumulation de phyto-toxines limitant la croissance des plantes et l'ammonium peut être toxique pour les plantes (par exemple, des concentrations en ammonium comprises entre 0,6 et 4,8 mg l⁻¹ induisent des réactions de stress ou inhibent la croissance des plantes).

Les plantes aquatiques sont également reconnues comme des organismes ingénieurs qui modifient activement leur habitat. Les taches représentent des zones de haute résistance à l'écoulement, qui conduisent à une déviation du flux d'eau au-dessus et/ou à côté des taches et à une augmentation de la vitesse et la turbulence au dessus et/ou sur les côtés des taches. L'écoulement traverse partiellement la canopée, mais avec une vitesse réduite. Les changements des conditions hydrodynamiques dues aux taches ont des effets indirects en cascade sur la dynamique des sédiments: la réduction de la turbulence à l'intérieur des taches favorise l'accumulation de sédiments fins. Au contraire, l'accélération de l'écoulement à proximité des taches empêche la sédimentation et contribue à la remise en suspension et à l'érosion des sédiments, conduisant à des sédiments similaires, voire plus grossiers par rapport aux zones sans végétation.

Les modifications induites de l'environnement physique par les plantes induisent des rétroactions positives à courte distance (à l'intérieur des taches) et des rétroactions négatives à distance (à côté des taches) pour les plantes elles-mêmes, conduisant à la formation des patrons régulières. Ces rétroactions échelle-dépendantes générées par l'interaction des plantes avec l'environnement physique expliquent donc l'expansion latérale des taches mais ne permettent pas d'expliquer leur développement dans la dimension longitudinale. Dans les environnements lotiques, les taches de différentes espèces de plantes aquatiques présentent le plus fréquemment des tailles intermédiaires (1-2 m de long), suggérant que les tailles des taches les plus fréquentes induisent une modification optimale des conditions environnementales auxquelles les plantes sont exposées. L'existence d'un seuil de taille minimale nécessaire pour induire des rétroactions positives pour les plantes et/ou d'un seuil de taille maximale au delà duquel des rétroactions négatives ont lieu n'a jamais été démontrée chez les végétaux aquatiques. Ces seuils pourraient être influencés par l'amplitude de la modification de l'environnement physique et biogéochimique induite par les plantes, elle même dépendante des traits des plantes et des caractéristiques architecturales des taches. Les caractéristiques des plantes et des taches devraient donc jouer un rôle important dans le contrôle des actions et rétroactions entre les plantes et l'environnement, avec des

conséquences importantes pour la dynamique des taches. L'objectif de ma thèse était d'étudier le rôle des caractéristiques architecturales des plantes et des taches dans les processus qui induisent des rétroactions positives et/ou négatives pour les plantes et comment les conditions environnementales affectent ces processus. Des mesures in situ de l'hydrodynamique, des caractéristiques des sédiments et de la morphologie des plantes ont été effectuées le long de l'axe central de taches de longueur croissante.

L'objectif du Chapitre 1 était d'étudier l'effet de la taille des taches sur les interactions entre les plantes, les écoulements et les sédiments dans les écosystèmes lotiques et de déterminer si ces effets différaient selon les caractéristiques environnementales. Des mesures in situ de la vitesse du courant et de la taille des particules du sédiment le long des taches de longueur croissante (L) de *Callitriche platycarpa* ont été effectuées sur deux sites présentant des caractéristiques d'écoulement et de sédiments différentes. Les résultats ont démontré qu'une taille minimale était nécessaire pour induire une réduction de la vitesse et une accumulation de sédiments fins dans la tache. La vitesse diminuait linéairement avec la longueur des taches, mais indépendamment des conditions du site. Au contraire, la texture des sédiments (taille des particules) dépendait plutôt des conditions du site: pour le site caractérisé par une vitesse plus élevée et des sédiments plus grossiers, la taille des particules diminuait exponentiellement avec la longueur des taches, atteignant une valeur minimale à $L \geq 1,0$ m, tandis que pour l'autre site la taille des particules atteignait une valeur minimale pour une longueur $L > 0,3$ m. Les résultats démontrent qu'une taille minimale de tache est nécessaire pour observer un effet des plantes sur la composante physique de l'environnement et que cet effet augmente avec la longueur des taches. Les petites taches induisent peu ou pas de modification de l'habitat physique et l'augmentation de la taille des taches conduit à des modifications de l'habitat de plus en plus importantes.

L'objectif du chapitre 2 était d'étudier les effets de la longueur des taches sur les processus biogéochimiques (accumulation/diminution des nutriments, respiration microbienne) et les rétroactions (positives ou négatives) sur les plantes elles-mêmes résultant de ces effets. Pour cela, des mesures de vitesses et des échantillonnages de sédiments, d'eau interstitielle et de plantes ont été réalisés in situ le long de taches de longueur croissante de *C. platycarpa* dans deux sites qui diffèrent par la vitesse d'écoulement, la taille des grains de sédiments et le niveau trophique. Les caractéristiques des sédiments, le taux de respiration microbienne, la

concentration en nutriments dans l'eau interstitielle et la taille des plantes ont été mesurés. Les résultats ont montré un effet significatif de la longueur des taches sur la teneur en matière organique dans les sédiments, les concentrations en nutriments dans l'eau interstitielle et les concentrations relatives d'ammonium et de nitrate. Pour les petites taches ($L < 0,9$ m), tous ces paramètres présentaient des valeurs proches de celles mesurées en amont. Pour les taches plus longues ($L \geq 0,9$ m), la concentration en matière organique dans les sédiments, les concentrations d'orthophosphates et d'ammonium augmentaient de manière importante par rapport aux sédiments sans végétation, tandis que la concentration de nitrates diminuait dans la tache. Les nitrates étaient la forme prédominante d'azote (95% -100% de l'azote total) dans les taches courtes ($L < 0,9$ m), alors que dans les longues taches ($L \geq 0,9$ m) l'ammonium prédominait (60-95% de l'azote total). Le taux de respiration des sédiments, indicateur de l'activité microbienne était plus élevé dans les longues taches que dans les courtes. Enfin, la hauteur des plantes était liée à la longueur de la tache selon un modèle quadratique, suggérant l'existence d'une rétroaction négative au delà d'une longueur seuil, probablement due à la concentration élevée en ammonium qui peut être toxique pour les plantes. Les longueurs au delà desquelles ont lieu des changements des processus biogéochimiques et des rétroactions négatives sont plus faibles dans l'écosystème avec le niveau de nutriments le plus élevé. Ce chapitre a démontré que les taches de plantes aquatiques, et en particulier les taches d'une certaine longueur, sont des *hotspots* biogéochimiques, avec des taux plus élevés de certains processus microbiens, intervenant dans les cycles des nutriments et de la matière organique. La régulation des processus biogéochimiques par la longueur des taches est également susceptible de contribuer à la dynamique des taches, en limitant dans certaines conditions la croissance des plantes et l'expansion des taches dans la dimension longitudinale.

Le chapitre 3 avait pour objectif de tester l'effet de deux espèces de plantes aquatiques sur les caractéristiques de l'écoulement et des sédiments. Pour cela, deux espèces ont été sélectionnées, *C. platycarpa* et *Elodea nuttallii*, car elles présentent des morphologies et des caractéristiques architecturales contrastées. Des profils de vitesse 3D et les caractéristiques des sédiments ont été mesurés le long de l'axe d'une tache de chaque espèce. Les deux espèces présentaient des effets contrastés sur la vitesse, sur les profils de turbulence et les caractéristiques des sédiments : la tache d' *E. nuttallii* présentait une accumulation de sédiments très fins principalement dans la première moitié amont et au centre de la tache alors que la tache de *C. platycarpa* induisait des effets significatifs sur l'hydrodynamique et l'accumulation de sédiments fins également en aval de la tache. Les résultats de ce chapitre

soulignent le rôle que la morphologie des plantes joue dans la modification de l'hydrodynamique et des caractéristiques physico-chimiques des sédiments induite par la présence de la végétation.

Mes recherches confirment que, dans les systèmes lotiques, les taches de plantes aquatiques ont un effet important sur l'habitat physique, en particulier sur l'hydrodynamique et les caractéristiques des sédiments, et démontrent, pour la première fois, que cet effet dépend de la taille des taches.

La réduction de la vitesse du courant et l'accumulation de sédiments fins ont des conséquences en cascade sur les processus biogéochimiques, l'ensemble étant fortement lié à la taille des taches. Mes recherches démontrent que des seuils de taille minimale sont nécessaires pour que 1) des rétroactions positives pour les plantes se produisent, puis, 2) au delà d'une certaine taille, que des rétroactions négatives apparaissent, limitant potentiellement la croissance des plantes et l'expansion des taches. Ces seuils devraient être plus courts pour les espèces ayant une canopée plus dense et plus élevée, car ces caractéristiques architecturales augmentent la capacité des taches de piéger les sédiments fins et la matière organique. L'effet que les taches ont sur la modification des vitesses du courant et sur les caractéristiques sédimentaires et biogéochimiques semble être un facteur important régulant la taille des taches et conduisant à une auto-organisation spatiale.

Avec l'augmentation du niveau trophique, les taches peuvent avoir un effet plus important sur les processus biogéochimiques de sorte que des rétroactions négatives apparaissent dans des taches plus courtes que dans des niveaux trophiques plus faibles, conduisant *in fine* à des distributions de taille de taches différentes selon le niveau trophique. Enfin, les taches de végétation aquatiques jouent un rôle important dans les cycles des nutriments, contribuant à la capacité d'autoépuration et à l'hétérogénéité des systèmes lotiques.

To my parents

To Fares

In memory of my dear friend Mauro Valtriani (1984 – 2016)

“I do not yet know why plants come out of the land
or float in streams,
or creep on rocks
or roll from the sea.
I am entranced by the mystery of them,
and absorbed by their variety and kinds.
Everywhere they are visible yet everywhere occult”

Liberty Hyde Bailey

“Water is the driving force of all nature”

Leonardo da Vinci

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1. Effects of patch length on biogeochemical processes	163
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INTRODUCTION

1. Regular pattern formation in stressful environments: ecosystem engineering, scale-dependent feedbacks and evolutionary consequences

The study of regular pattern formation and their dynamics is one of the major subjects in ecology. A pattern, or patchiness, is a set of spatially distinct patches, which were defined by Forman (1995) as “relatively homogeneous non-linear areas that differ from their surrounding”. The study of patch dynamics focuses on the processes driving patch development and the interactions between patches and their surrounding (Pringle *et al.* 1988). In ecological systems, patchiness can be physical, when the abiotic characteristics and resources have a patchy distribution, or biological, when vegetation and animal communities are distributed in regular patterns (Pickett *et al.* 1999). Biological patchiness has been observed in stressful environments for a wide range of organisms, particularly vegetation as bushy vegetation in arid ecosystems, shrubs and trees in nutrient-limited savannahs, tussock vegetation in freshwater intertidal wetlands, trees in alpine environments, and other organisms as mussel beds in intertidal zones and benthic diatoms in intertidal mudflats (Rietkerk and van de Koppel 2008 and reference therein).

Vegetation patchiness can be caused by the physical patchiness (*e.g.* heterogeneity in soil properties or local topography), but it can also be observed in homogeneous environmental conditions. Rietkerk and van de Koppel (2008) proposed that the regular pattern formation for biological communities in homogeneous conditions, called spatial self-organisation, can be caused by interactions with other organisms or the environment occurring at different scales. Spatial self-organisation can be caused by organisms through opposite biological interactions (*e.g.* facilitation and competition), resource redistribution or modification of the physical habitat occurring at different spatial scales. Certain organisms, defined as physical ecosystem engineers, interact with the environment by physically modifying the abiotic characteristics of the environment and inducing feedbacks for themselves or for other species (Jones *et al.* 1994, 1997; Hastings *et al.* 2007). Ecosystem engineering often occurs in stressful environments (Jones *et al.* 1997) and can be considered as a strategy enabling organisms to cope with stress (Bouma *et al.* 2010, see Box 1 for the definition of stress). The feedbacks resulting from the engineer-environment interactions can be positive (*e.g.* stress alleviation or increased availability of resources) or negative (*e.g.* stress aggravation or reduced availability of resources) (Jones *et al.* 1997). When feedbacks occur at different scales, being positive at short distance and negative at a long distance (*i.e.* scale-dependent feedbacks), the

Box 1 Stress and disturbance in lotic systems

The term **stress** is defined as “the external constraints which limit the rate of the dry matter production of all or a part of the vegetation” (Grime 2002). In lotic system, flow is a source of stress principally through the hydrodynamic forces that are exerted on aquatic plants and other organism in general (Puijalon and Bornette 2013).

Disturbance consists in any process that limits plant biomass through its major destruction (Pickett and White 1985; Trémolières 2004). For examples, extreme changes in flow (*e.g.* draughts or floods) can be source of disturbance for lotic ecosystems.

engineering may lead to the formation of regular patterns (or patchiness), even in homogenous environmental conditions (Rietkerk and van de Koppel 2008), generating spatial self-organisation. Physical ecosystem engineers are able to redistribute the physical or nutrient stress (Jones *et al.* 1997), by the in-patch alleviation of stress, resulting into a local facilitation (Bertness and Hacker 1994; Bruno *et al.* 2003). Instead, in the patch surroundings, stress is accentuated, inhibiting patch developments. This latter long-distance negative feedback is fundamental for the formation of regular patterns, contrary to short-distance positive feedbacks that, alone, do not represent a sufficient condition to create patchiness (van de Koppel and Crain 2006; Rietkerk and van de Koppel 2008). The strength and spatial extent of the scale-dependent feedbacks depend on the intensity of stress to which ecosystem engineers are exposed to, together with the organism traits involved in engineering (*e.g.* mechanical properties) (Bouma *et al.* 2013), as the organism traits specifically controls the ecosystem engineering capacity of the organism (Bouma *et al.* 2005; Bouma *et al.* 2009, see Box 2).

On a long-term perspective, the action of the ecosystem engineer could change the selective pressure of the environment through continuous modifications of the environment, therefore influencing the evolution of the ecosystem engineer itself (Gutiérrez and Jones 2001; Erwin 2008). This evolutionary process is called niche construction, and physical ecosystem engineering is only one of the possible mechanisms of niche construction (Gutiérrez and Jones 2001; Matthews *et al.* 2014). Niche construction is defined as a process whereby organisms, through informed activities, modify their own and the population niches (Odling-Smee 1988; Odling-Smee *et al.* 2013). Niche constructor organisms modify the selective pressure experienced in their environment, for instance through habitat choice, resource consumption or the physical modification of the environment (Gutiérrez and Jones 2001; Odling-Smee *et al.* 2013). In particular, for the physical ecosystem engineers, the organism evolution does not depend only on the abiotic characteristics of the environment and

Box 2 Traits, performance and fitness

The term **trait** indicates any morphological, physiological or phenological characteristic that is measurable at the individual level, without mentioning the environmental factors or any other levels of organisation (Violle *et al.* 2007). A trait within a species can show different values (also call attributes) along different environmental conditions or through time (Lavorel *et al.* 1997; Violle *et al.* 2007).

The term **performance** refers to the relative efficiency of an organism to carry out a specific function in determined environment conditions (Koehl 1996, 2010). According to the **paradigm of ecomorphology**, proposed by Arnold (1983) for animals and revisited for plants by Violle *et al.* (2007), certain traits, called **functional traits**, have direct or indirect effects on the performance of the organism in the environment. The performance, in its turn, has a direct or indirect influence on the fitness of the organism. **Fitness** is defined as the adaptedness of an organism to its environment (Sultan 1987) and it can be assessed by its ability to growth, reproduce and survive. For a particular plant species in a particular ecological habitat, fitness can be estimated through the **performance traits**: vegetative biomass, reproductive output (*e.g.* seed number) and plant survival (Koehl 1996; Violle *et al.* 2007).

Certain functional traits are relevant for the plant-environment interactions (Lavorel and Garnier 2002; Lavorel *et al.* 2007; Gross *et al.* 2008). The **response traits** present different attributes in response to environmental conditions (Lavorel and Garnier 2002; Violle *et al.* 2007). Plant height and leaf nutrient concentrations are examples of response traits to nutrient resources in sediments, to disturbance and other environmental conditions (Lavorel *et al.* 1997). The **effect traits** reflect the effects of a plant on the environment. Shoot stiffness is an example of morphological trait with influences the capacity of aquatic plants to reduce hydrodynamic forces of waves and currents (Bouma *et al.* 2005).

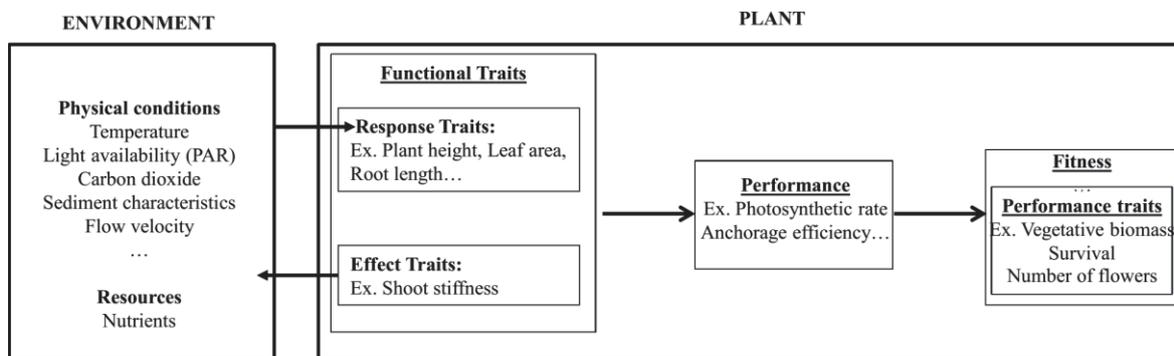


Fig. I. Relations between the environment, the functional traits, the performance, and the fitness of a plant.

the biological interactions, but also on the modification that the organisms themselves produce within their environment (Corenblit *et al.* 2009). Similarly to feedbacks induced by ecosystem engineering that can be positive or negative, the niche constructor can increase the niche by mitigating selective pressures (*i.e.* niche construction) or reduce the niche by increasing the selective pressure (*i.e.* niche destruction) (Vandermeer 2008; Odling-Smee *et*

al. 2013). Following the niche construction concept, the ecosystem engineer and the environment co-evolve together through continuous interactions and feedbacks (Corenblit *et al.* 2008). It is consequently fundamental to integrate the niche construction concept for the understanding of patch dynamics in stressful environments and, on a larger spatial and temporal scale, of the evolution of the ecosystems (Corenblit *et al.* 2009).

2. Regular pattern formation in lotic systems: the case of aquatic vegetation

The patchy distribution of aquatic vegetation in lotic systems (Fig.1) has been documented for a long time (Hynes 1970; Sand-Jensen and Madsen 1992). However, regular patterns formation generated through scale-dependent feedbacks have been only recently recognised for submerged aquatic vegetation in lotic systems (Schoelynck *et al.* 2012). In the following paragraphs, the lotic systems and aquatic plants are introduced, reviewing the adaptations of submerged aquatic plants to lotic environments, and the interactions and feedbacks that lead to the vegetation patch formation in lotic systems are discussed (Fig.2).

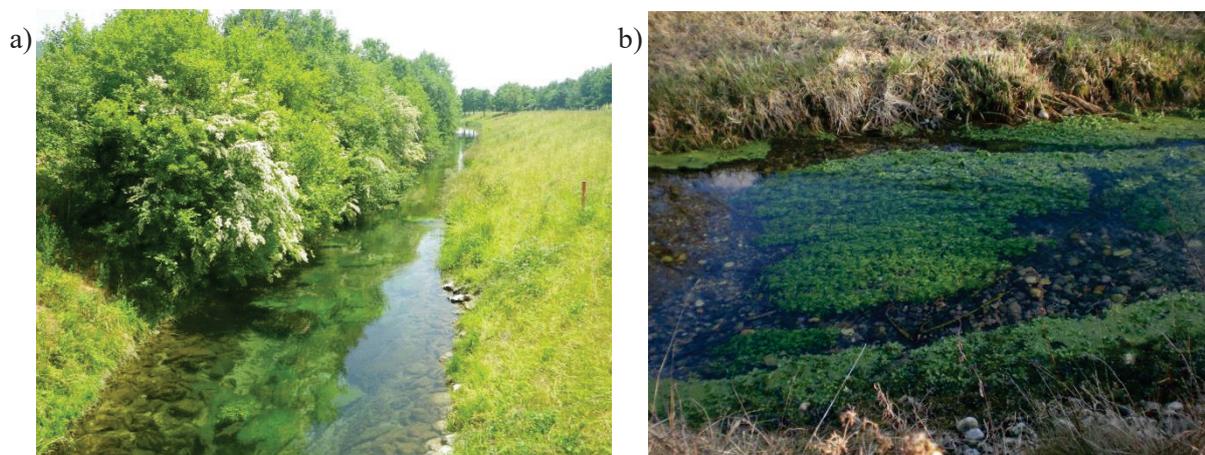


Fig. 1. a) Vegetation patterns of submerged aquatic vegetation of *Callitriche platycarpa*, and b) patches of *Veronica anagallis-aquatica*.

2.1. The lotic system: a stressful environment

Lotic systems are freshwater ecosystems characterized by a unidirectional water flow, including natural and altered ecosystems with widely different hydraulic, morphologic and biologic characteristics. The flow is one of the main environmental factors that drive the structure and the biological processes occurring in lotic systems, through interactions occurring along four dimensions (Ward 1989). The longitudinal dimension includes the

upstream-downstream interactions. The lateral dimension consists of interactions between the channel and riparian/floodplain systems. The vertical dimension is characterised by interactions between the surface water and the groundwater systems. Finally, time represents the fourth dimension that defines the temporal scale at which the interactions in the other dimensions occur.

Spatial and temporal heterogeneity of the abiotic and biotic factors is a fundamental characteristic that influences patterns and processes in lotic systems (Palmer and Poff 1997). Lotic ecosystems are considered to be stressful environments mainly due to the permanent unidirectional flow, which can cause mechanical damages to organisms, as for instance their dislodgment (Riis and Biggs 2003), and to the high spatial and temporal variability of the abiotic factors (Trémolières 2004). Organisms living in lotic systems, such as submerged aquatic plants, present strategies and adaptations that enable them to tolerate and spread in such conditions (Barrat-Segretain 1996; Puijalon *et al.* 2011; Puijalon and Bornette 2013).

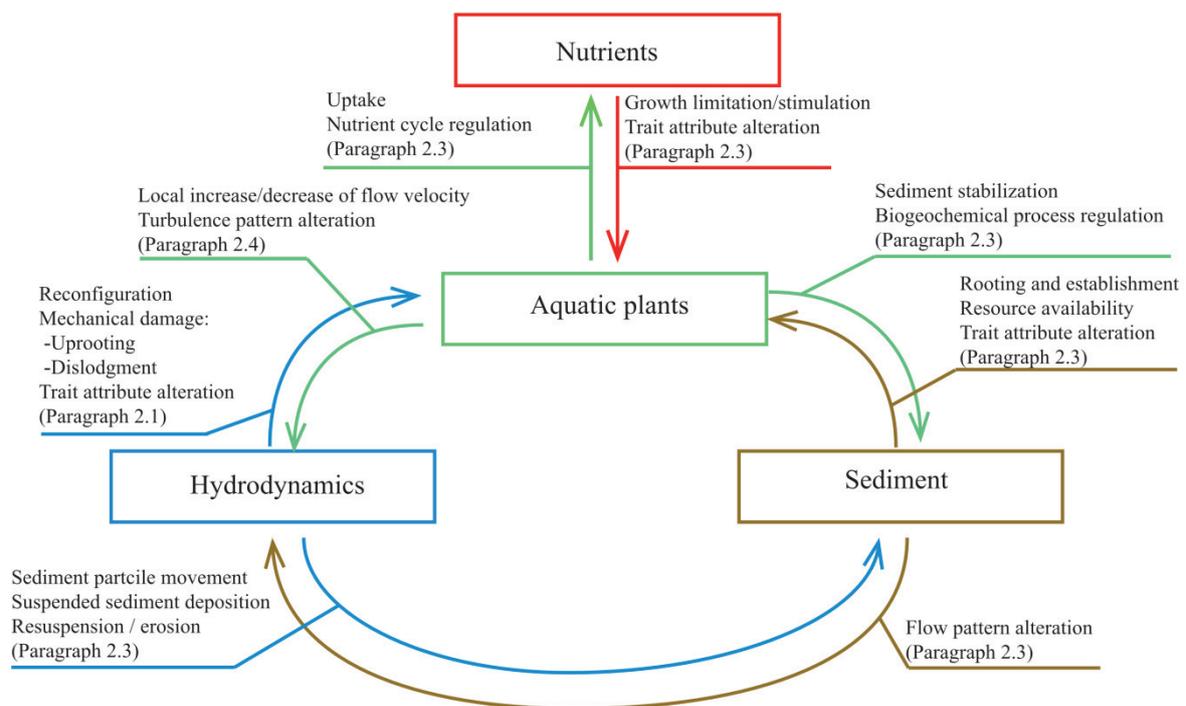


Fig. 2. Conceptual models representing the interactions and feedbacks that form a feedback loop for the aquatic vegetation and the abiotic components in lotic systems. Submerged aquatic plants influence and are influenced by the hydrodynamics, the sediment characteristics and the nutrients characteristics that constitute the lotic ecosystems. The different colours correspond to the different components of the feedback loop and their actions on other components (green for submerged aquatic plants, blue for the hydrodynamics, brown for sediment and red for nutrients). In the parentheses is indicated the paragraph of this chapter in which the interaction is discussed.

2.2. Submerged aquatic plants and their adaptation to lotic environments

The term submerged aquatic plants refers to freshwater plants growing completely submerged and usually anchored to the substratum with roots or anchoring organs (Haslam 1978; Chambers *et al.* 2008). Submerged plants are fundamental primary producers of freshwater ecosystems that provide food and shelter to others species but also influence flow patterns, sedimentation processes and regulate biogeochemical cycles (Wetzel 1964; Pip and Robinson 1984; Lodge 1991; Sand-Jensen 1998; Wigand *et al.* 2001; Clarke 2002; Strayer and Malcom 2007). Submerged aquatic plants are therefore important elements of lotic environments, contributing to the habitat structure and heterogeneity, biodiversity and ecological functioning of these ecosystems (Haslam 1978; Dawson 1988; Champion and Tanner 2000; Franklin *et al.* 2008).

Effect of flow velocity on submerged aquatic vegetation

The growth and development of aquatic plants and their communities in lotic ecosystems are strongly influenced by water flow (Haslam 1978; Dawson 1988; Janauer 2001; Madsen *et al.* 2001). Extremely high flow velocities ($> 1 \text{ ms}^{-1}$) preclude the development of aquatic vegetation (Puijalon and Bornette 2013 and reference therein). At intermediate flow velocities, aquatic vegetation is usually distributed in distinct mono-specific patches (Hynes 1970; Sand-Jensen and Madsen 1992), while extremely low flow velocities ($< 0.1 \text{ ms}^{-1}$) allow the development of aquatic vegetation characteristic of lentic waters presenting a more uniform distribution (Dawson 1988; Sand-Jensen and Madsen 1992; Puijalon and Bornette 2013).

Flow in lotic systems induces a permanent drag on rooted submerged plants (Vogel 1984; Sand-Jensen 2003; Puijalon *et al.* 2005; O'Hare *et al.* 2007; Puijalon *et al.* 2008; Puijalon *et al.* 2011), which are pulled in the flow direction. Drag depends both on water velocity and on plant morphological characteristics (Usherwood *et al.* 1997; Vogel 2003; Puijalon and Bornette 2013). Drag can cause mechanical damage, uprooting and dislodgment to plants (Riis and Biggs 2003). The type of damage caused by drag depends not only on drag but also on the mechanical properties of plants and sediment cohesion (Schutten *et al.* 2005).

Survival and reproduction strategies to hydrodynamic forces

Submerged aquatic plants have developed several strategies that enable them to tolerate hydrodynamic forces and spread in lotic conditions. These strategies occur both at an

individual level (*e.g.* morphological and biomechanical characteristics) and at a patch level (*e.g.* density, shape of the patch) and basically consist in avoiding the stress generated by flow and in increasing the tolerance to the mechanical forces (Puijalon *et al.* 2011; Puijalon and Bornette 2013).

At an individual level, some plants are able to avoid the stress by having a small size or linear strap-like and thin leaves (Sand-Jensen 2003; Puijalon and Bornette 2004). These morphological adaptations maintain a low frontal area, minimizing plant drag (Vogel 1984). Drag reduction can also be due to the flexibility of aboveground organs, which are able to deform according to current velocity, reducing thus their roughness and frontal area (Vogel 1984, 1994; Schutten and Davy 2000). This plant streamlining in the flow direction with stems and leaves closely compressed to minimize canopy volume is called reconfiguration (Schutten and Davy 2000; Sand-Jensen and Pedersen 2008; Puijalon and Bornette 2013). Other individual strategies that enable submerged aquatic plants to survive in lotic ecosystems consist in tolerating drag by increasing the resistance to breakage of stems and leaves (Biehle *et al.* 1998 ; Miler *et al.* 2010) and by increasing their resistance to uprooting (Schutten *et al.* 2005).

Stems and leaves breakage implies a reduction of fitness for plants. Submerged aquatic plants have adapted to lotic systems, where the risk of breakage is high, through an enhanced capacity to regenerate both from underground organs and fragments. Regeneration is a kind of vegetative reproduction, which is frequent for aquatic plants and can even totally substitute sexual reproduction (Barrett *et al.* 1993; Barrat-Segretain 1996; Santamaría 2002). Vegetative reproduction allows the recolonisation of disturbed habitats and the colonisation of downstream habitats (Barrat-Segretain 1996; Barrat-Segretain *et al.* 1998; Mony *et al.* 2011). Vegetative reproduction can occur clonally by rhizomes, runners or stolons, and lead to the formation of aquatic vegetation patches (Sand-Jensen and Madsen 1992; Schoelynck *et al.* 2017).

The formation of patches in aquatic plants represents also a strategy alleviating the stress for individuals. A dense patch, constituted by many individual plants, acts as a single obstacle to flow, concentrating high water velocities on the upstream and lateral edges of the patch and therefore providing a mutual protection against flow for the individuals inside the patch (Sand-Jensen and Madsen 1992; Schoelynck *et al.* 2013). In particular, dense patches of flexible species have the capacity to reconfigure their canopy and reduce patch height with increasing flow velocity minimizing the patch drag (Sand-Jensen and Pedersen 2008). Elongated, streamlined patches of flexible submerged vegetation are usually observed in lotic

systems (Sand-Jensen and Pedersen 2008), whereas less flexible species, adopting principally a tolerance strategy, usually tend to form more open patches and colonize low flow habitats (O'Hare *et al.* 2007).

Phenotypic plasticity as an adaptation to the high heterogeneity of lotic systems

Species of submerged plants in lotic ecosystems present the morphological and mechanical traits that allow both individual plants and patches to have good performances (see Box 2 for definition) in the environmental conditions to which they are usually exposed to. Lotic environments are characterised by a high spatial and temporal variability of habitat conditions (Palmer and Poff 1997). Aquatic plants are adapted to the spatial and temporal heterogeneity due to a large phenotypic plasticity (Santamaría 2002; Peralta *et al.* 2005). Phenotypic plasticity is defined as the capacity of a genotype to express different phenotypes in different environments (Sultan 2000). For example, the same genotype of submerged plant could present differences in the morphological and biomechanical traits (*e.g.* plant height, leaf size and flexibility) depending on the water velocity to which they are exposed to, resulting in high performances in the different conditions (Puijalón and Bornette 2004; Puijalón *et al.* 2005; Puijalón and Bornette 2006). Phenotypic plasticity in submerged aquatic plants occurs also in response to other factors (*e.g.* sediment and nutrients) that play an important role in plant growth and distribution.

2.3. Other abiotic factors influencing submerged plant growth in lotic environments: sediment characteristics, nutrient availability and synergic effects of flow, sediment and nutrients

Sediment in lotic systems

The bed of lotic systems can be characterized by different substrata. Most channels bed are constituted of not consolidated material called sediment (Haslam 1978). Sediment is porous, permeable and therefore saturated of water. The layer of saturated sediment directly in contact with the flowing water of a lotic system is termed hyporheic zone (Orghidan 1959; Boano *et al.* 2014). The main characteristic of the sediment is the grain size, usually classified by the Wentworth scale in fluvial ecology (Wentworth 1922; Cummins 1962). Depending on its grain size and the flow characteristics, sediment can move above the bed rolling, sliding, by saltation, by traction, can be suspended with the flow or remain in place. For this reason,

flow characteristics play an important role in the grain size distribution of the bed sediment (Butcher 1933). Sediment characteristics are important for lotic systems. Through their texture (*i.e.* the particle size distribution and the proportions of the various size ranges of particles, Hillel 1998) and porosity, sediments control the exchange with the subsurface waters in the hyporheic zone, thus influencing the rate of oxidation of sediment (Findlay 1995). Indeed, coarse sediments facilitate the exchange of water between the surface and the hyporheic zone, whereas fine sediment slow down the water exchanges (Wondzell 2011). In the areas where the bed of the lotic system is convex, as in the head of riffles, the surface water moves down into the hyporheic zone (*i.e.* downwelling; Hendricks and White 1988), whereas in the areas where the bed is concave, as at the end of riffles, the hyporheic water moves toward the bed surface (*i.e.* upwelling; Hendricks and White 1988). Moreover, sediment texture controls the organic matter content (Hargrave 1972; Findlay 1995). Sediments also influence the flow dynamics through their roughness, in particular by modifying the turbulence conditions and consequently also the processes of deposition and resuspension of the finest material. Finally, the chemical characteristics of sediment (*e.g.* nutrient composition, content in organic material) influence the habitat of benthic organisms, such as aquatic vegetation and macroinvertebrates.

Effect of sediment characteristics on submerged aquatic vegetation

The sediment characteristics influence the growth, morphology and distribution of aquatic plants (Boeger 1992; Koch 2001). In particular, sediment stability controls the rooting and establishment of aquatic vegetation (Butcher 1933; Haslam 1978; Franklin *et al.* 2008), while sediment texture and porosity influence the nutrient and oxygen availability for the underground organs through the control of porewater exchanges with the surface water. Fine sediments, as sediments enriched in silt and clay, are less permeable to water and richer in nutrients compared to coarser sediments as coarse sand and gravel (Haslam 1978; Koch 2001). The organic matter content in sediment influences plant growth: a low-level increase of organic matter content improves the nutrient availability in the sediment favouring plant growth (Sand-Jensen and Søndergaard 1979), whereas high concentrations of organic matter content inhibit plant growth (Barko and Smart 1983; Barko and Smart 1986; Lehmann *et al.* 1997). High concentration of organic matter can be toxic for plants potentially through different interacting mechanisms, as, for instance, the presence of anaerobic conditions and consequent low root oxygenation and the high concentrations of phytotoxins (Barko and Smart 1986 and references therein).

Nutrients in lotic ecosystems

The dissolved compounds present in the waters of a lotic system depends on the geological characteristics of its drainage basin and the processes occurring therein, such as the atmospheric processes, the biological processes and the anthropic activities (Clarke 1920; Luc 1986; Hedges *et al.* 1994). The processes occurring locally in the lotic systems also play a key role in the regulation of the nutrient cycles, controlling the concentration and forms of nutrients that are exported downstream (Meyer and Likens 1979). In lotic systems, the biogeochemical cycles depends on water movement on the longitudinal dimension and the exchange with the hyporheic zone in the vertical dimension: the dissolved nutrients continuously move downstream according to the water velocity, they are transported and retained in the hyporheic zone where they can be sequestered by plants or transformed by microorganisms before returning to the water column possibly in another form (Newbold *et al.* 1981; Ensign and Doyle 2006). Nutrient cycling is fundamental for the correct functioning of lotic systems, as it controls the nutrient availability for the organisms. Nutrient availability regulates the development of aquatic vegetation and other primary producers. Some nutrients, in particular nitrogen and phosphorus (which cycles are described in Box 3 and 4) can be present in low concentrations in natural lotic ecosystems, thus limiting plant growth. In limiting nutrient conditions, the plant growth is enhanced when the concentration of the limiting nutrient is increased (Madsen and Cedergreen 2002). Rooted submerged plants are able to uptake nutrients both by root and leaves, from sediment and water column

Box 3. Nitrogen cycle in lotic ecosystems

Nitrogen is abundant in the atmosphere as diatomic nitrogen (N_2) but unavailable to most organisms. In freshwater systems, only some cyanobacteria are able to transform the diatomic nitrogen in molecules available for organisms, as ammonia (NH_3), through a process termed **nitrogen fixation**. In aqueous solution, the ammonia concentrations are regulated by an acid-base equilibrium. At the pH values frequently observed in lotic systems (6-8), the ammonium ion (NH_4^+) prevails on NH_3 . Under oxic conditions, ammonium is transformed by chemoautotroph bacteria firstly in nitrite (NO_2^-) and then in nitrates (NO_3^-) through a two steps process termed **nitrification** (Verstraete and Focht 1977; Schmidt 1982). The two steps are coupled and effectuated by different microorganisms. Low oxygen concentrations limit nitrification with consequent ammonium accumulation (Dahm *et al.* 1987; Kemp and Dodds 2001). Nitrates and ammonium can be easily assimilated by microorganisms and aquatic plants. Once assimilated, the inorganic nitrogen is transformed in organic nitrogen, making the nitrogen in this latter form available for other organisms (*e.g.* macroinvertebrates, fishes). Oppositely, all the organisms are able to convert organic nitrogen in ammonia by a process termed **ammonification** (Ladd and Jackson 1982). The nitrogen cycle is completed by a microbial process, called **denitrification**, which transforms nitrates back to diatomic nitrogen. Denitrifying bacteria use nitrates for their respiration process in anoxic conditions (Verstraete and Focht 1977; Seitzinger 1988). As an anaerobic respiration, denitrification is accompanied by a transformation of organic matter in carbon dioxide. Figure II summarizes the nitrogen cycling occurring in lotic systems. The nitrogen is not only produced locally: it is imported from upstream, introduced by the lateral connection by runoff, and, possibly come from upwelling of underground water. Similarly, the dissolved nitrogen is exported downstream, or disappears in the downwelling of water entering in the aquifer or can be exported laterally by flood episodes.

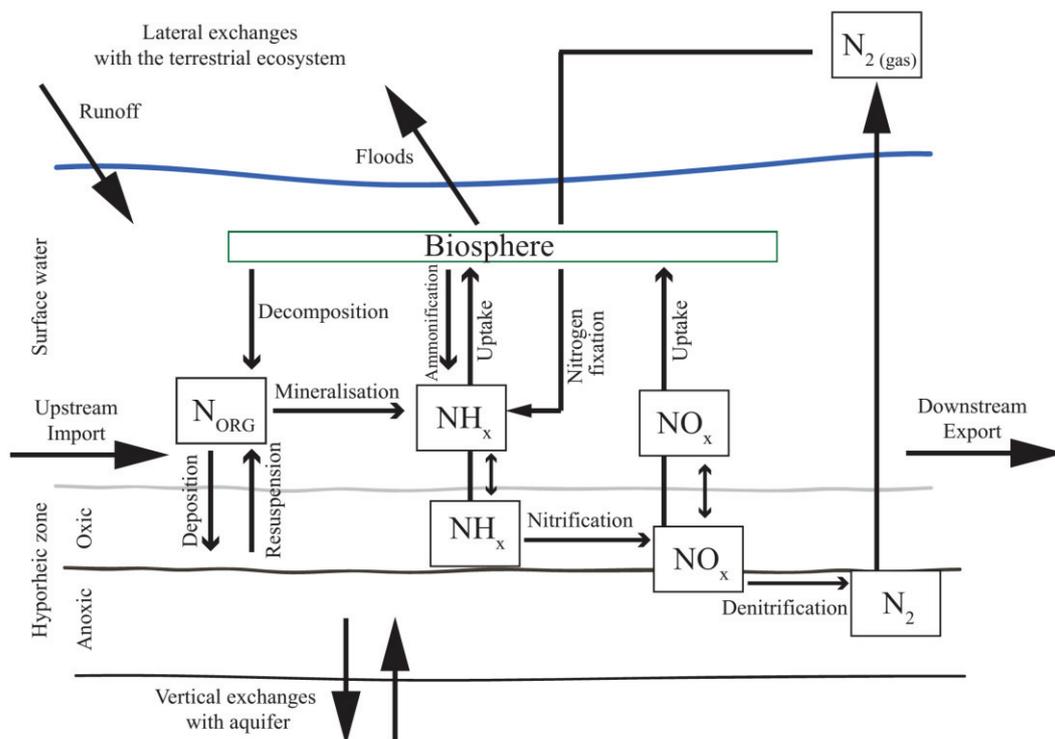


Fig. II: Schematic representation of the nitrogen cycle in lotic ecosystems.

Box 4. The phosphorus cycle in lotic systems

Most of the phosphorus is localised in the sediments and the principal source of phosphorus is the apatite minerals present in rocks. However, the phosphate contented in this mineral has an extremely low solubility. Apatite phosphates are solubilized through the action of weathering, microorganisms and plants (Ruttenberg 2003 and reference therein). The soluble forms of phosphorus are the phosphoric acid (H_3PO_4) and its ions. In aqueous solutions the concentrations of the different ions of phosphoric acid are regulated by the following acid-base equilibrium:



At the pH values frequently observed in freshwater ecosystems (6-8), the predominant ions are the dihydrogen phosphate (H_2PO_4^-) and the monohydrogen phosphate (HPO_4^{2-}). In these soluble forms, phosphorus can be easily assimilated by organisms, which convert soluble phosphates in organic phosphorus. After the dead of organism, the organic phosphorus is partly recycled in soluble forms by decomposition, while the other portion is mineralized back as apatite. For lotic ecosystems, the terrestrial inputs are an important source of phosphorus: particulate phosphorus (as both organic and inorganic forms) and, in minor quantity, dissolved phosphates are transported to the lotic system by runoff (Ruttenberg 2003; Filippelli 2008). If not promptly assimilated by organisms and converted in organic phosphorus, the soluble phosphates are easily removed from the solution through different geochemical processes: orthophosphate can form insoluble compound and then co-precipitate with other ions (e.g. Ca^{2+} , Mg^{2+} , Fe^{3+}), with ferric-oxhydroxides (FeOOH) or it can be adsorbed by clay, therefore reducing the availability for uptake by organism. Under anoxic conditions, that can occur in highly organic sediments, some microorganisms are able to reduce Fe(III) into Fe(II) : the insoluble salt FePO_4 is transformed in the soluble $\text{Fe}_3(\text{PO}_4)_2$ and the FeOOH is reduced in the more soluble hydroxides, as Fe(OH)_2 , increasing the bioavailability of the orthophosphate. Adsorbed phosphorus can precipitate and be deposited and, if not resuspended, it can be buried in sediment and be temporarily sequestered from the cycle.

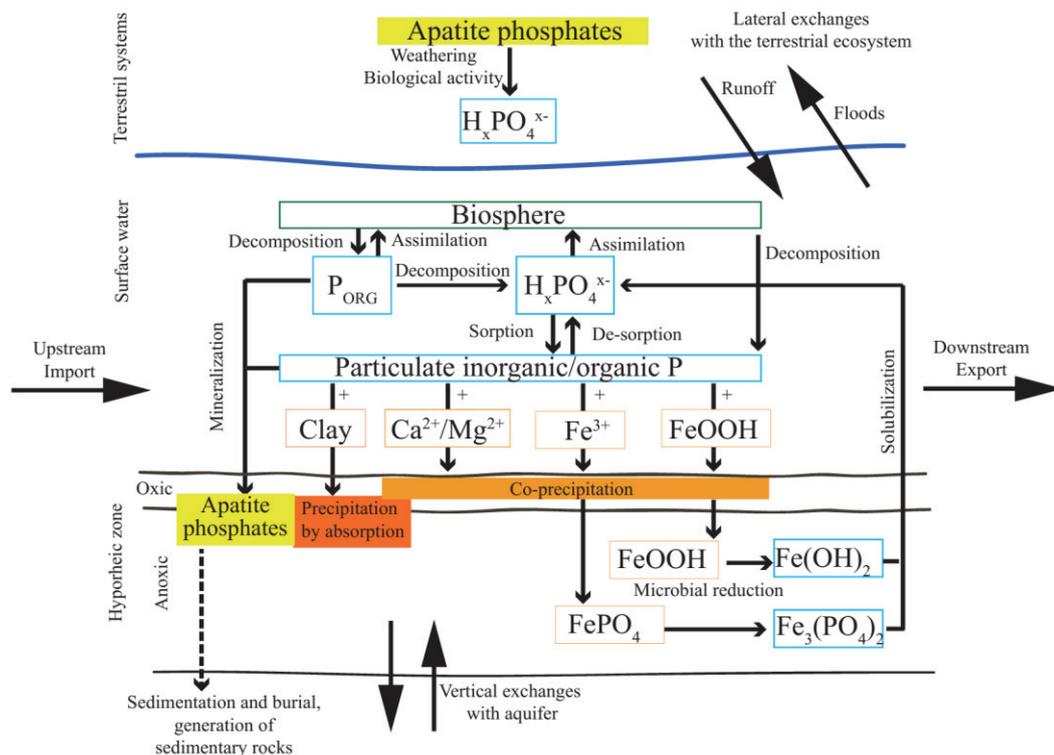


Fig. III. Schematic representation of the phosphorus cycle in lotic ecosystems. The phosphorus soluble forms are indicated by the light blue color.

respectively, preferring the source with higher nutrient availability (Nichols and Keeney 1976; Madsen and Cedergreen 2002). In natural systems, plants should present higher uptake of nitrogen and phosphorus from the sediment, as the interstitial water of sediment is usually richer in these nutrients compared to open water (Barko and Smart 1986; Barko *et al.* 1991).

High concentration of certain nutrient can be also toxic for plants. Even if ammonium represents a fundamental nutrient and source of nitrogen for aquatic plants (Nichols and Keeney 1976; Barko *et al.* 1991; Xie *et al.* 2005), ammonium can be a possible phytotoxin for aquatic plants in freshwater systems (Britto and Kronzucker 2002; Clarke and Baldwin 2002; Nimptsch and Pflugmacher 2007). Depending on species sensitivity, relatively high ammonium concentrations may inhibit plant growth (Clarke and Baldwin 2002; Cao *et al.* 2009; Yu *et al.* 2015) and photosynthesis (Rudolph and Voigt 1986; Su *et al.* 2012), induce oxidative stress (Cao *et al.* 2004; Nimptsch and Pflugmacher 2007; Cao *et al.* 2009) and lead to internal carbon-nitrogen imbalance (Cao *et al.* 2009).

Phenotypic plasticity in response to sediment characteristics, nutrient availability, and interactive effect of flow, sediment and nutrients

Both nutrient availability and sediment texture influence the morphology of aquatic plants. Aquatic plants show a broad phenotypic plasticity in response to nutrient availability and sediment texture. In coarse sediments (*e.g.* sand), poorer in nutrients compared to finer sediments, aquatic plants present longer and thinner roots and an increased root allocation (Wolfer and Straile 2004; Xie *et al.* 2005). These phenotypes may enhance nutrient acquisition efficiency under poor nutrient conditions (Wolfer and Straile 2004; Xie *et al.* 2005). It has also been demonstrated that high nutrient concentrations lead to weaker stem tissues compared to low nutrient concentrations (Lamberti-Raverot and Puijalón 2012). In addition, some studies demonstrated an interactive effect of nutrients or sediment characteristics and flow on plant morphology and plant growth (Boeger 1992; Idestam-Almquist and Kautsky 1995; Puijalón *et al.* 2007). Boeger (1992) demonstrated that in sandy sediments, the highest growth of a submerged plant was observed for intermediate velocities, while at low and high velocities submerged plant showed lower growth. On the contrary, submerged aquatic plants rooted in mud showed high level of growth at all velocities (Boeger 1992). Puijalón *et al.* (2007) demonstrated that, a submerged plant could show contrasting morphologies in response to increased water velocities depending on nutrient concentrations (*e.g.* smaller size or larger size at low or high nutrient concentrations respectively). Therefore,

the exposure of submerged plants to several abiotic factors, as it occurs in natural lotic systems, can induce complex responses.

2.4. Effects of submerged plant patches on the lotic environment

Submerged aquatic plants represent the largest sessile organisms in freshwater environments, acting as physical ecosystem engineers (Carpenter and Lodge 1986; Jones *et al.* 1994, 1997; Hastings *et al.* 2007). Submerged plants are established at key interfaces in lotic systems. Fundamental physical and biogeochemical processes occur at the plants-flow-sediment interfaces (Carpenter and Lodge 1986; Marion *et al.* 2014).

First of all, submerged plant patches represent a region of high flow resistance, which causes the flow to deflect and accelerate above and/or next to the canopy, locally increasing water velocity and turbulence at the top and/or the edges of the patch (Fig.3a) (Sand-Jensen and Mebus 1996; Nepf and Vivoni 2000; Sand-Jensen and Pedersen 2008). Patches are porous structures: flow partially passes through the patch, but with a reduced velocity relative to the upstream (Sand-Jensen and Mebus 1996; Sand-Jensen and Pedersen 2008; Vandenbruwaene *et al.* 2011). The processes of flow deflection away from the patch and flow deceleration within the patch occur over an adjustment length at the leading edge of the patch (Chen *et al.* 2013). Beyond this adjustment length, the velocity, shear stress and turbulence are generally reduced inside plant patches (Sand-Jensen and Pedersen 1999; Baptist 2003; James *et al.* 2004).

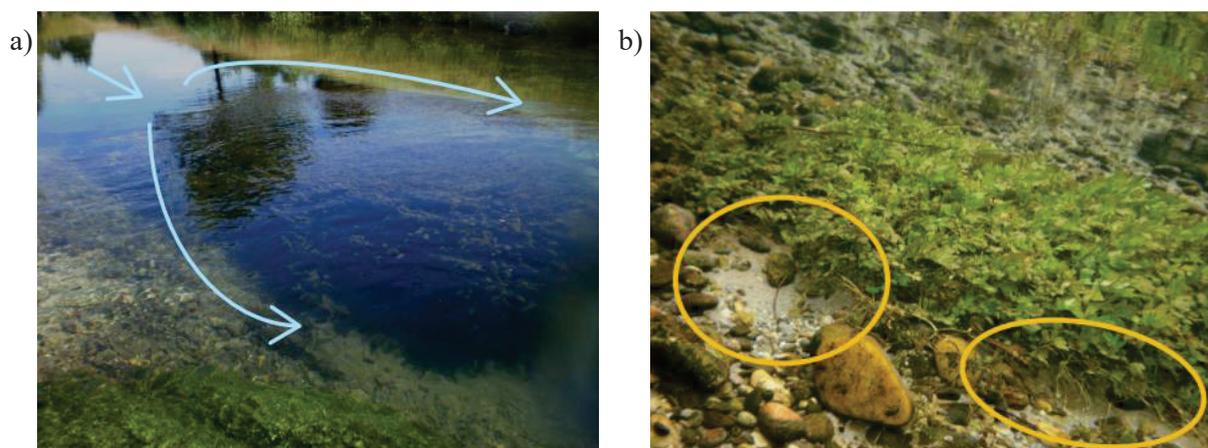


Fig. 3. Effects of submerged aquatic patches on the physical habitat in lotic ecosystems: a) flow deflection by a patch of *Elodea* sp. And b) accumulation of fine sediment under a patch of *Berula erecta*.

The changes in hydrodynamic conditions due to the effects of plant on flow have indirect cascading effects on sediment dynamics: the reduction of turbulence inside plant patches favours sedimentation by reducing the potential of resuspension and erosion, with consequent reduction of water turbidity too (Sand-Jensen 1998; Schulz *et al.* 2003; Hendriks *et al.* 2009). In addition, suspended and bed-transported particles may be directly trapped inside plant patches due to collision with shoots (Gacia *et al.* 1999; Pluntke and Kozerski 2003; Hendriks *et al.* 2008). As a consequence, sediment tends to accumulate inside plant patches, with an increased proportion of fine particles compared to bare areas (Fig. 3b). Simultaneously, flow acceleration next to the patch impedes sedimentation or even contributes to particle resuspension and erosion, resulting in similar or even coarser sediment compared to bare areas (Sand-Jensen 1998; Schoelynck *et al.* 2013).

The role of traits on the modifications of physical environment

The plant-induced modifications of the physical environment depend on plant morphology and patch architectural characteristics. For instance, at the plant level, the leaf area index (ratio of leaf surface area to the ground area covered by the plant canopy) has a significant effect on the amount of fine sediment accumulated in submerged patches (Petticrew and Kalff 1992). Shoot stiffness influences the physical modifications of the habitat: reconfiguration of patches of flexible plants tends to minimize the surface area in contact with water, reducing the patch resistance to flow (Sand-Jensen 2003; O'Hare *et al.* 2007; Miler *et al.* 2012), and to push the canopy close to the sediment, potentially promoting sediment retention (Sand-Jensen and Pedersen 2008). At a patch level, species with dense canopies induce a high reduction of flow velocity inside their patches, increasing sediment retention, whereas species with open canopies have less impact on flow and sediment dynamics (Sand-Jensen and Mebus 1996; Sand-Jensen 1998). However, only few studies have investigated simultaneously the effect of different plant morphologies and patch architectures on both flow and sediment characteristics (Sand-Jensen 1998). A minimum patch density is necessary to produce sufficient habitat modification triggering positive feedbacks for the engineer (Bouma *et al.* 2009). Patch size has been shown as a fundamental architectural characteristic that influences the flow velocity and sediment stability in salt marshes patches: a minimal patch size is required to reduce water velocity and stabilize the sediment within plant patches and the magnitude of these modification increases with patch length (Bruno and Kennedy 2000; Bos *et al.* 2007). However, no study has investigated the role of patch size on habitat modification for

submerged vegetation in lotic ecosystems. Whereas salt marshes plants, which are emergent, as exposed to waves and tides, the unidirectional flow is the only source of hydrodynamic stress for submerged vegetation in lotic environments. As they are exposed to different constraints, the effect of patches on the physical habitat and the processes regulating patch size may differ.

In conclusion, plant traits and patch architectural characteristics are key factors governing the capacity of aquatic plants to modify the physical environment, by influencing the intensity and scale of their interactions with the environment (Bouma *et al.* 2013).

Consequences of the modifications of physical environment by plants on the biogeochemical processes

The modification of the physical environment induced by plants may have important implications for biogeochemical processes (Gutiérrez and Jones 2006). 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) and to sediment enrichment in organic matter and nutrients as nitrogen and phosphorus (Dahm *et al.* 1987; Sand-Jensen 1998; Schulz *et al.* 2003; Horvath 2004), compared to coarser sediments next to the patch. Inside the patch, the high organic matter content of sediment supports decomposition processes, resulting in an enhanced sediment oxygen demand (Hargrave 1972) and, consequently, reduced oxygen concentrations. The reduced oxygen availability for microbial processes (Sanders *et al.* 2007) may induce a shift from aerobic to anaerobic process (Gutiérrez and Jones 2006). Particularly, for nitrogen, the establishment of anoxic conditions should inhibit the nitrification process, which requires oxygen to transform the ammonium in nitrate and contemporary enhance the denitrification process, which is an anaerobic respiration. In conclusion, the modification of the physical habitat induced by submerged aquatic plants may also influence microbial processes, which in turn may regulate the nutrient availability for the plants. Up to now no study investigated the effects of plant-induced modifications of the physical habitat on the biogeochemical processes. Moreover, the growth of submerged aquatic plants should be regulated through feedbacks triggered by physical habitat modifications (Horvath 2004), self-regulating hydrodynamic stress, light availability, sediment characteristics and nutrient availability by physical ecosystem engineering.

2.5. Feedbacks for plants

The interactions between plants, flow, sediment, and nutrients composed of actions and feedbacks, can be schematized as a feedback loop (Fig. 2). The plant-induced modifications of the physical environment trigger short-distance (*i.e.* inside the patch) positive feedbacks and long-distance (*i.e.* alongside the patch) negative feedbacks for the plants themselves (Schoelynck *et al.* 2012). Patches have an effect on all the feedback loop components, influencing hydrodynamics, sediment characteristics and nutrient availability. The effect of plant can be direct on a component of the feedback loop and be the results of cascading effects on other components, with effects both inside and next to the patch. As a consequence, plant growth and thus patch expansion could be locally enhanced inside the patch (Sand-Jensen 1998) and reduced next to the patch leading to regular pattern formation (Schoelynck *et al.* 2012; Schoelynck *et al.* 2013). The scale-dependent feedbacks generated by the interaction of submerged plants with the physical environment explain therefore the mechanisms that limit the lateral expansion of submerged patches (Schoelynck *et al.* 2012). On the other hand, the mechanisms that control patch growth on a longitudinal dimension are still unexplained. Indeed, in lotic environments, patches occur at a wide range of sizes. Sand-Jensen (1998) and Schoelynck *et al.* (2012) reported many patches of intermediate size (1-2 m long) and fewer patches of other sizes, for different species of submerged aquatic vegetation in lowland streams. This size distribution of natural patches is still unexplained, and it suggests that the most frequent patch sizes in the system may induce an optimal modification of the environmental conditions to which they are exposed. For submerged aquatic vegetation in lotic environments, neither the existence of a minimal size threshold necessary to trigger positive feedbacks for plants, as it has been done for salt marsh patches (Bruno and Kennedy 2000; Bos *et al.* 2007), nor a maximal size threshold over which negative feedbacks for plants would occur have been demonstrated. The presence of these size thresholds may explain the natural patch size distribution in lotic environments. These thresholds are probably influenced by the level of modification of the physical environment induced by aquatic plants and the cascading effect on the biogeochemical conditions, both process being mediated by the plant traits and patch architectural characteristics (Bouma *et al.* 2013). Plant traits and patch characteristics should have, therefore, an important role in controlling the feedback loop with important consequences for the patch dynamics.

3. Aims and objectives

The aim of my thesis was to study the role of plant and patch architectural characteristics in the processes that trigger positive and/or negative feedbacks for plants and how the nutrient level affects these processes. These questions are addressed on plant patches in lotic ecosystems. Here, the permanent unidirectional flow influences the plant-induced processes of physical habitat modifications, with potential cascading effects for the biogeochemical processes. Previous studies in lotic systems focused mainly on the lateral dimension of the scale-dependent feedbacks generated by hydrodynamic forces and erosion and sedimentation processes (Schoelynck *et al.* 2012), while the questions of this work will be addressed on a longitudinal dimension.

My thesis is structured in three parts:

- 1) The first part focuses on the effects of patch size on the physical habitat modifications induced by plants and how these effects vary in lotic system with different water velocity and sediment characteristics. This part investigates the effect of patches of different sizes on both flow and sediment texture.
- 2) The second part focuses on the effect of patch size on biogeochemical processes (*i.e.* accumulation/depletion of nutrient, nitrification and denitrification, microbial respiration) in patchy ecosystems and on the feedbacks for plants. This part investigates whether the effects of patch size on hydrodynamics and sediment has cascading consequences on the biogeochemical processes within aquatic patches, and eventually on plant growth.

Particularly, in these first two parts, it was investigated whether there are patch size thresholds that may induce positive or negative feedbacks for the plant themselves along the patches.

- 3) The third part evaluates the effects of two submerged plant species having contrasting morphologies on different directional components of flow velocity and sediment characteristics. This part investigates the role of morphology and patch structure on the physical habitat modifications induced by aquatic plants.

MATERIALS AND METHODS

1. Patch sampling strategies

The study units of this work are patches of submerged vegetation. I selected mono-specific patches that were well defined (with sharp edges) and isolated from surrounding bare areas or other vegetation patches, corresponding to the first category of patches defined by Schoelynck *et al.* (2017). This type of patches is usually developed from few individual plants which, after their establishment, have expanded clonally (Schoelynck *et al.* 2017). The dimensions of the patches studied varied from very short patches (0.16 m long), composed of a dozen rooted plants, to long patches, over 3 m long, covering the full range of observed lengths in the sites. Investigating patches of increasing length allowed investigating whether there are patch size thresholds over which positive or negative feedbacks for plants occur and understanding the consequences for the patch dynamics (Chapter 1 and 2).

During the spring-summer 2014, natural patches were sampled in drainage channels of the Upper Rhône River (France), near the localities of Brégnier-Cordon (45.6452 N, 5.6080 E), Serrières-de-Briord (45.8153 N, 5.4269 E) and Peyrieu (45.6765 N, 5.6773 E) (Fig. 4). These artificial drainage channels present a more uniform structure (cross-section, water depth, and sinuosity) than natural channels while being naturally colonized by submerged aquatic vegetation. The channels are fed by the Rhône river seepage and hillslope aquifers. The type of channel feeding and their management keep the channel discharge relatively stable, especially in spring and summer season. Some parameters regarding channel geomorphology, depth-averaged and time-averaged velocity, sediment characteristics and water physico-chemical characteristics of the three channels are reported in Table 1.

Working on these sites represented an improvement over experimentations under controlled conditions, such as flume studies, as it allowed studying established vegetation that had been exposed to natural environmental conditions but also enabled also to reduce the complexity of conditions that can be found in natural streams (*e.g.* higher sinuosity, flow spatial and temporal variability).

SITE (Abbrev.)	Brégnier-Cordon (LV)	Serrières-de-Briord (HV)	Peyrieu (PEY)
Z_{Ch} (m)	0.8	1.3	0.7
W_{Ch} (m)	6.0	8.0	4.7
U (m s⁻¹)	0.13 ±0.01	0.20± 0.01	0.15±0.03
d_{0.3} (µm)	78 ±26	123±29	194±53
OM (%)	2.20±1.41	1.35±0.86	1.77±1.16
Λ (µS cm⁻¹)	374±2	447±2	446±15
T (°C)	13.7±0.3	14.4±0.3	12.4±1.03
pH	8.1±0.2	8.3±0.2	7.36±0.42
PO₄³⁻ (ppb)	37.4±11.0	53.1±10.6	20.61±16.23
NH₄⁺ (ppb)	19.3±3.5	22.3±3.5	11.05±12.65
NO₃⁻ (ppm)	3.6±0.9	11.05±12.65	9.70±4.25
IBMR (trophic level)	10.51 (moderate)	9.55 (poor)	9.57 (poor)

Table 1. Description of the three sites studied: channel geomorphology (maximum channel depth (Z_{Ch}) and width (W_{Ch})); depth-averaged and time-averaged velocity (U); sediment characteristics (fine fraction expressed as a percentile value ($d_{0.3}$) and organic matter content (OM)); surface water physico-chemical characteristics (conductivity (Λ), temperature (T), pH, concentration of orthophosphate (PO_4^{3-}), ammonium (NH_4^+) and nitrate (NO_3^-)); trophic level (Macrophyte Biological Index for Rivers (IBMR), Haury *et al.* 2006).

2. Species investigated

I worked on two different species of submerged aquatic plants: *Callitriche platycarpa* Kütz. and *Elodea nuttallii* (Planch.) St.-John. These two species were chosen as they present contrasting morphologies and patch architectural structures (Fig. 5). *C. platycarpa* has densely packed leaves, forming a rosette at the shoot apex, resulting in the concentration of the most of the biomass 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 due to the entanglement of stems (Tison and de Foucault 2014). Patches of *C. platycarpa* usually present an elliptical structure and the patch height increases along the patch length. Long patches (usually over 1m long) present an over-hanging canopy, created by the long, flexible and buoyant stems extending in the downstream direction. Consequently, long patches are rooted only in the upstream part.

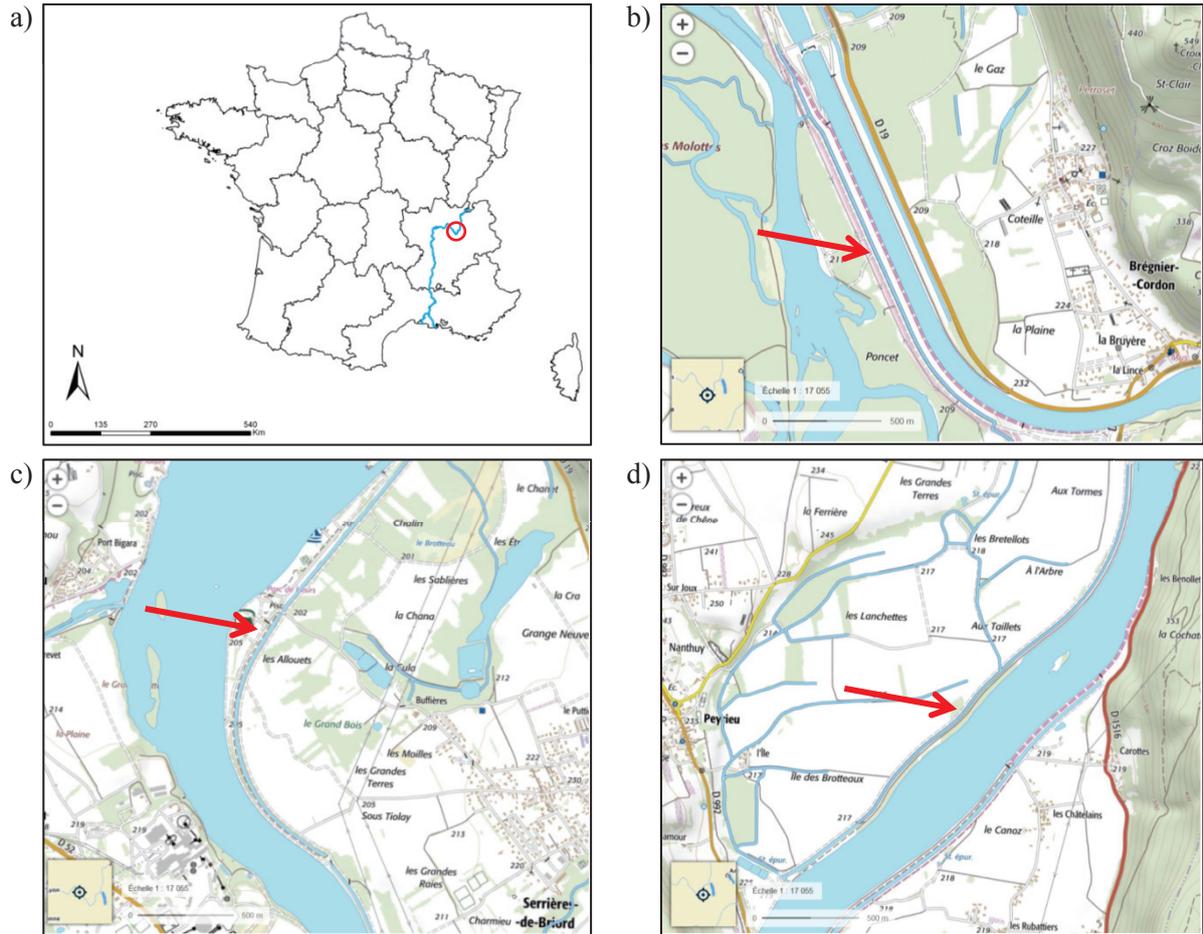


Fig. 4. a) Localisation of the sites (red circle) along the Upper Rhône river (in light blue). The drainage channels near the locality of Brégner-Cordon (b), Serrières-de-Briord (c), Peyrieu (d) indicated by the red arrows, where vegetation patches were studied (IGN maps, <http://www.ign.fr/>; <https://www.geoportail.gouv.fr/>).

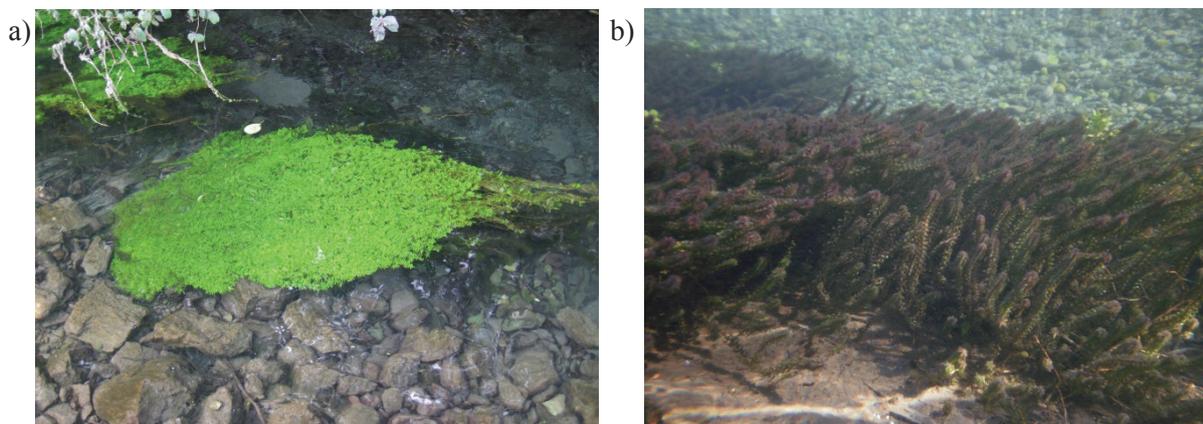


Fig. 5. Patches of a) *C. platycarpa*, and b) *E. nuttallii*. The patch of *C. platycarpa* presents an increased height on the upstream part of the canopy (left side of the picture), while the patch of *E. nuttallii* presents a more compact structure with a constant height.

E. nuttallii has relatively rigid stems, 10-50 cm up to 150 cm long (Tison and de Foucault 2014), with few or no ramifications. Stems present three-leaved whorls densely packed and distributed almost uniformly along all their length. Patches of *E. nuttallii* are dense and compact with an elongated shape in direction of the flow and do not present an overhanging canopy.

C. platycarpa was chosen because firstly its patchy distribution has been recognized as spatial-self organization (Schoelynck *et al.* 2012) and secondly because it is largely present in monospecific patches in the study sites. I used this species to investigate the role of patch length on the modification of the physical habitat and its consequences for the biogeochemical processes and the plant responses (Chapter 1 and 2).

E. nuttallii was chosen for its contrasting morphology and patch architectural characteristics from *C. platycarpa*. The two species were studied in Chapter 3 to investigate the role of plant traits and patch characteristics on the physical habitat modification.

3. Field sampling and measurements

For each sampled patch, coupled measurements of hydrodynamics and sediment collection were carried out along the central axis of the patch. The sampling positions included points outside the patch, at the bare sediment, and within the patch. Bare sediments upstream of the patches were taken as a reference for flow and sediment characteristics in absence of vegetation. The comparison between the upstream bare sediment and the in-patch sediments allows investigating the habitat modifications induced by plant patches. For each position, a velocity profile was measured, a core of sediment and interstitial water samples were collected for sediment characterization and plant specimens were harvested to perform a morphological analysis. These measurements were chosen to provide descriptions of the physical habitat (Chapter 1, 2, and 3), the biogeochemical processes occurring in the sediment (Chapter 2), and the consequent plant responses (Chapter 2).

3.1. Hydrodynamics

The measures of 3D vertical velocity profiles and the relative turbulence intensity allow understanding the effects of the patches on hydrodynamics in term of flow pattern

modification and flow acceleration/deceleration. On the other side, flow velocity represents a proxy for the mechanical stress acting on plants.

Velocity vertical profiles were measured using a 3D Acoustic Doppler Velocimeter (ADV, FlowTracker Handheld-ADV, SonTek USA). This instrument is a good compromise between precision and portability: the FlowTracker can measure water velocities from 0.0001 to 4.0 m s⁻¹ with a 1Hz sampling rate. It offers the performance of an ADV, while allowing data collection in the field from a simple handheld interface without the use of a computer.

Vertical profiles consisted in depth-steps of less than 12 cm, reduced to 1-4 cm near plants-water-sediment interfaces. Due to the dimensions of the side-looking probe and its support, measurements closest to the sediment were taken at a minimum of 4cm above the channel bed (Sand-Jensen and Pedersen 1999). Velocity was recorded over 100s at 1Hz. This time of measuring was chosen as a compromise between the measurements of the temporal variability of the velocity, and the limited time needed to complete all the measurements on one single patch in a single day. For each component of velocity (streamwise, u ; spanwise, v ; vertical, w), time-averaged velocity profiles (\bar{u} , \bar{v} , \bar{w}) were obtained. In Chapter 1 and 2, from each time-averaged velocity profile, the velocity at 20 cm above the bed, \bar{u}_{20} , was estimated by interpolation. This distance was chosen to avoid bottom interference due to the presence of boulders and cobbles. Moreover, this choice allowed us to measure hydrodynamic forces faced by plants during their growth and the patch development in relation to the patch architecture. 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 of depth were located above the canopy for the smallest patches and at the upstream end of long patches. In these cases, \bar{u}_{20} may qualitatively capture changes in the velocity field due to lateral deflection of flow away from the patch, but they will definitely over-estimate the velocity within the canopy. In Chapter 3, the turbulence intensity was quantified as the velocity variation around the mean (standard deviation). The standard deviation was then divided by the mean velocity to calculate the relative turbulence intensity.

3.2. Sediment characterisation

Sediment grain size

Particle size distribution was used as physical characterisation of the sediment samples. The comparison of grain size distribution curves and sediment texture allowed understanding the plant-induced modifications of the fine textural fraction of sediment

between bare sediment and within-patch sediments. The difference in the fine textural fraction between the two types of sediments is a proxy for the fine sediment accumulation or erosion occurring within the patches.

Grain size analyses of sediment were carried out in the aqueous phase by laser diffractometry, using a Malvern Mastersizer 2000 G (diameter range: 0.01 -2000 μm). The analytical model used is based on the Fraunhofer theory and considers particles equal to spheres. Sediment samples were sieved at 1600 μm prior to analysis. As sediment samples were dried at 70°C to allow their preservation, sediments were sonicated for 2min to destroy the aggregated particles formed during the drying process (Badin *et al.* 2009). The results of the analysis give the complete array and distribution of particle sizes which are displayed as grain size distributions curves. The mode of the curve indicates the most abundant grain size in terms of the percentage per total solid volume. The curves were transformed into cumulative curves, and the percentile values $d_{0.1}$, $d_{0.3}$, $d_{0.5}$ were calculated (maximum diameter corresponding to 10%, 30%, and 50%, respectively, of the total particle volume). The three values were found to be correlated, and only the percentile value $d_{0.3}$ was kept for further analyses.

Organic matter content and carbon to nitrogen ratio

The organic matter content of sediment samples was measured by weight loss after ignition at 550°C for 2 hours (LOI, Dean 1974). The organic matter content gives indications of the carbon sources available for the biogeochemical processes of decomposition and denitrification. Organic matter in sediment consists of a labile (metabolizable) and a refractory (non-metabolizable) fraction (Ittekkot 1988). We measured the C:N ratio in order to assess the quality of the organic matter content in the sediment. Low values of C:N indicate a fresh and highly labile organic matter. On the contrary, high values of C:N indicate an organic matter that has been already processed by the microbial organisms and that is therefore refractory. In order to measure the C:N values, for each sediment sample, two sub-samples were finely grounded, acidified with HCl (2mol l⁻¹) and then placed in ultra-light-weight silver capsules to measure the total nitrogen and total carbon by an elemental analyzer (FlashEA; Thermo Fisher Scientific, Waltham, MA, USA).

Interstitial water chemical characteristics

Interstitial water was sampled with a 60 ml syringe used to pump water inside a screened mini-piezometer (1 m long, 1.7 cm diameter, and 5 cm screen length) pushed 20cm deep inside the sediments using an internal metallic rod (Dahm *et al.* 1996; Lefebvre *et al.* 2005). Interstitial water chemical characteristics were analysed within 48 hours, based on standard colorimetric methods, measuring ammonium (EPA Method 349, 1997, US Environmental Protection Agency, Washington, DC), orthophosphate (EPA Method -600/4-79-020, 1983), nitrate and nitrite concentration (EPA Method 352.2, 1993), using an automatic analyser (Easychem Plus; Systea, Anagni, Italy).

These parameters were chosen as they enable to estimate the nutrient cycling occurring in sediment, as they depend on the oxygen availability, microbial processes and plant uptake. Orthophosphate concentrations are the results of the balance between the uptake by plants and microorganisms and the processes of adsorption/precipitation or desorption/solubilisation which occur respectively in oxic and anoxic conditions (Dahm *et al.* 1987). Ammonium concentrations are resulting from the balance between the processes of ammonification, nitrogen fixation, nitrification, denitrification and the uptake by both plants and microorganisms. The accumulation of ammonium is observed under anoxic conditions as a result of the inhibition of the aerobic processes consuming ammonium (*i.e.* denitrification; Dahm *et al.* 1987). Nitrate concentrations give an indication of the balance between the nitrate uptake by both plants and organisms, and the balance between the nitrification, which produce nitrates in oxic conditions, and denitrification, which consumes nitrates in anoxic conditions, while the consumption of nitrates by dissimilatory nitrate reduction to ammonium (DNRA) is most likely negligible in lotic systems (Silvennoinen *et al.* 2008).

Nutrient concentrations also give an indication of the nitrogen and phosphorous availability for plant uptake by roots, which are essential nutrients for the plant growth (Koerselman and Arthur 1996). Extreme nutrient concentrations may induce negative effects for plants: low nutrient concentrations may limit plants growth and, oppositely, high concentrations of ammonium can be toxic for plants. Depending on aquatic plant species sensibility, relatively high ammonium concentrations (0.6-4.8 mg l⁻¹) may inhibit plant growth and photosynthesis, induce oxidative stress and lead to internal carbon-nitrogen imbalance (Rudolph and Voigt 1986; Clarke and Baldwin 2002; Cao *et al.* 2004; Nimptsch and Pflugmacher 2007; Cao *et al.* 2009; Su *et al.* 2012; Yu *et al.* 2015).

Microbial respiration rate

The microbial respiration rate of sediment is a proxy for the aerobic microbial activity for processes of decomposition and nitrification. Certain microorganisms consume oxygen for the processes of decomposition of the organic matter as a source of carbon, or to obtain energy from the oxidation of ammonium to nitrate (*i.e.* nitrification). Therefore microbial respiration rate is dependent on the quantity and quality of organic matter available for the decomposition processes and the availability of inorganic carbon and ammonium for the nitrification processes. These processes occur mainly at the sediment surface, where oxygen is available in high concentration.

To measure the microbial respiration rate, within 24 hours from sediment collection, three subsamples of 5 ml of fresh sediment collected from the surface of each corer. The subsamples were incubated to measure the potential sediment microbial respiration rate ($\mu\text{g}_{(\text{O}_2)} \text{h}^{-1} \text{g}_{\text{dry sed}}^{-1}$). Sediment sub-samples were incubated in bottles of 125 ml sealed by a double cap and filled with site water previously saturated in oxygen and placed under controlled conditions (15 °C, dark, and stirring to avoid O₂ depletion) for 15 h ca. For each subsample, the oxygen consumption was calculated by measuring O₂ concentration at the beginning and at the end of the incubation by optical dissolved oxygen sensor (HQ40D; Hach, Loveland, CO, USA). Once the incubation was finished, each subsample was reversed in an aluminium cup previously weighted and then dried at 70°C until constant weight was reached to measure the exact dry weight of each subsample.

3.3. Plant morphology

Plants were stored in sealed plastic bags saturated with water in a climate room at 19°C for maximum 48 h until they were analyzed. For each plant sampled, we measured plant height with a ruler and its mean value was calculated for two different positions in the patch: upstream of the patch (10% of patch length) and downstream of the patch (90% of patch length). Plant height was chosen as it represents a proxy for plant growth and is recognized as a functional trait integrating the plant responses to hydrodynamical stress and sediment resources (Puijalón *et al.* 2008; Puijalón *et al.* 2011) but also the plant effects on the biogeochemical cycles (Lavorel *et al.* 2007).

RESULTS

CHAPTER 1

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

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Abstract

Submerged aquatic plants are ecosystem engineers that are able to modify their habitat. However, the role of patch size in the engineering capacity of aquatic plants has not yet been fully investigated, while it could be essential for elucidating patch dynamics. Our objectives were to investigate the effects of patch size on plant-flow-sediment interactions in lotic ecosystems and to determine whether these effects differed according to environmental characteristics.

We performed in situ measurements of velocity and grain size along natural patches of increasing length (L) at two sites presenting different flow and sediment characteristics. Our results indicated that a minimum patch size was needed to induce in-patch streamwise velocity reduction and fine sediment accumulation. Streamwise velocity decreased linearly with L independently of the site conditions. The sediment texture was instead dependent on site conditions: for the site characterized by higher velocity and coarser sediment, the sediment grain size exponentially decreased with L , reaching a minimum value at $L \geq 1.0$ m, while for the site characterized by lower velocity and finer sediment, it reached a minimum value already at $L > 0.3$ m. This study demonstrated that a minimal patch size is required to trigger the ecosystem engineering capacity of aquatic plant patches in lotic environments and that this capacity increases with patch length. Small patches induce little to no modification of the physical habitat, with possible negative feedbacks for plants. With increasing patch size, the habitat modifications induced by plants become more important, potentially triggering positive feedbacks for plants.

Introduction

Rooted submerged aquatic plants are fundamental components of lotic freshwater ecosystems. These primary producers ensure the functioning of the ecosystem, regulating nutrient cycles, increasing habitat heterogeneity and serving as shelter and habitat for other organisms (Carpenter and Lodge 1986). As ecosystem engineers (*sensu* Jones et al. 1994), they play an essential role in aquatic ecosystems: rooted submerged plants modify flow conditions and sedimentation patterns (Sand-Jensen 1998; Sand-Jensen and Pedersen 1999), and some species are able to release oxygen into the substrate through their roots, influencing the availability of nutrients and microbial activity and hence biogeochemical processes in the substrate (Caffrey and Kemp 1992; Sand-Jensen et al. 1982; Soana and Bartoli 2013).

In streams, aquatic plants commonly form mono-specific patches (Sand-Jensen and Madsen 1992). The formation of patches is due to clonal growth, occurring mainly in the

downstream direction (Puijalon et al. 2008; Sand-Jensen and Madsen 1992). In addition to light and nutrient availability, patch expansion also depends on flow conditions and sediment characteristics, as well as the frequency and intensity of flood events, which may contribute to plant and patch uprooting (Bornette and Puijalon 2010; Franklin et al. 2008). Simultaneously, aquatic plant patches modify the flow of running water habitats, which in turn modifies sediment patterns and characteristics.

Patches represent a region of high flow resistance, which causes the flow to deflect and accelerate above and/or 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). Because the patches are porous, some flow can pass through the patch, but with a reduced velocity relative to the upstream (Sand-Jensen and Mebus 1996; Sand-Jensen and Pedersen 2008; Vandenbruwaene et al. 2011). The processes of flow deflection away from the patch and flow deceleration within the patch occur over an adjustment length, X_D , at the leading edge of the patch, which can range from 10 cm to several metres depending on the stem density and geometry of the patch (Chen et al. 2013). Beyond this adjustment length, the velocity, shear stress and turbulence are generally reduced inside plant patches (James et al. 2004; Sand-Jensen and Pedersen 1999), leading to a reduced potential of resuspension and erosion (Hendriks et al. 2009). Moreover, because turbulent diffusion is needed to keep particles in suspension, the reduction of turbulence inside plant patches also favours sedimentation (Hendriks et al. 2009; Sand-Jensen 1998; Schulz et al. 2003). Finally, suspended and bed-transported particles may be directly trapped inside plant patches due to collision with stems and leaves (Hendriks et al. 2008; Pluntke and Kozerski 2003). As a result of the processes above, sediment tends to accumulate inside plant patches, with an increased proportion of fine particles compared to bare areas, where flow acceleration next to the patch contributes to particle resuspension and erosion (Sand-Jensen 1998; Schoelynck et al. 2013). The plant-induced modifications of the physical environment trigger positive feedbacks for the plants themselves: as the hydrodynamic stress is reduced, the risk of mechanical damage and uprooting is also minimized, while the sediment, enriched in silt particles, enhances the availability of nutrients for plants. As a consequence, plant growth and thus patch expansion are enhanced.

The ecosystem engineering capacity of aquatic plants to modify flow conditions and to influence sediment particle deposition and erosion depends on plant morphology, *e.g.*, flexibility and stem density (Bouma et al. 2009; Sand-Jensen 1998) but also on patch geometry, such as its length, width and height relative to water depth (Nepf 2012). Patch

geometry influences flow velocity both inside (Sand-Jensen 1997; Schoelynck et al. 2014) and outside patches (Sand-Jensen and Mebus 1996; Sand-Jensen and Pedersen 2008), therefore also influencing sedimentation and the accumulation of organic matter (Schoelynck et al. 2012). For instance, for *Callitriche platycarpa*, a freshwater species, the acceleration next to the patch has been negatively related to the canopy depth of submergence and positively to the length/width ratio (Schoelynck et al. 2013), and wider patches present enhanced turbulence downstream of the patch compared to narrower, more streamlined ones (Sand-Jensen and Mebus 1996; Sand-Jensen and Pedersen 2008). For *Spartina alterniflora*, a salt marshes species, velocity reduction and substrate stabilization at the rear of the patch have been demonstrated to be positively related to patch size (Bruno and Kennedy 2000).

Some studies have shown that modifications of flow and sedimentation induced by plant patches depend not only on plant morphology and patch structure but also on hydrodynamic forcing (Bouma et al. 2009; van Wesenbeeck et al. 2008). Specifically, these studies showed that the flow acceleration and erosion adjacent to the patches are negligible under low water velocity and become more important with increasing water velocity. At the same time, another study demonstrated very similar flow patterns for similar patches exposed to different water velocities (Sand-Jensen and Pedersen 1999). These contradictory results indicate that the influence of flow velocity on the modification of flow and deposition by plant patches is still unclear. More importantly, the effect of some key abiotic (*i.e.*, sediment physico-chemical characteristics) and biotic (*i.e.*, patch size) parameters on these processes and their consequences for patch dynamics have not yet been fully investigated.

Plant patch dynamics and their effects on ecological processes across longitudinal, lateral and temporal gradients are still little studied in lotic ecosystems (Winemiller et al. 2010). Investigating plant patches of increasing size can elucidate patch dynamics through time, as increased patch size corresponds to increased age. In streams, patches occur at a wide range of sizes. Sand-Jensen (1998) and Schoelynck et al. (2012) reported many patches of intermediate size (1-2 m long) and fewer patches of other sizes, for *Callitriche* spp. and other aquatic species in lowland streams. This size distribution of natural patches is still unexplained, and it suggests that the most frequent patch sizes in the system may induce an optimal modification of the physical forcing to which they are exposed. However, most of the previous studies examining the effect of patch size on associated processes considered intermediate-sized patches, with a length from 1 to 2 m (Sand-Jensen and Pedersen 1999; Schoelynck et al. 2013), which prevents identifying thresholds or shifts occurring at smaller or larger patch sizes. In particular, it is still unknown what minimum size threshold is needed

to induce sufficient changes in flow and sedimentation to create positive feedback within the river channel patches, as demonstrated for circular patches in salt marsh environments (Bouma et al. 2007; Bruno and Kennedy 2000). Similarly, the factors that may limit the growth of aquatic plant patches in streams beyond a certain length are still unknown.

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

To test these hypotheses, we performed in situ measurements of velocity and grain size along natural patches of *Callitriche platycarpa*, considering patches of increasing length at two different sites. These sites differ in mean flow velocity and sediment grain size and

hence allow the consistency of the processes across different site conditions to be investigated.

Materials and methods

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) and Serrières-de-Briord (45.8153 N, 5.4269 E). These artificial drainage channels were selected because they present a more uniform structure (cross-section, water depth, low sinuosity) than natural channels while being naturally colonized by submerged aquatic vegetation. These channels are fed by Rhône river seepage and hillslope aquifers. The type of channel feeding and their management keep the channel discharge particularly stable, especially in spring and summer season. Cover by aquatic vegetation ranges from 30% to 90% depending on the season and channel section.

The two sites presented different mean velocities and sediment textures. In the sampling days, depth-average and time-average velocities were higher in Serrières-de-Briord than in Brégnier-Cordon ($0.20 \pm 0.01 \text{ ms}^{-1}$ and $0.13 \pm 0.01 \text{ ms}^{-1}$, respectively, t-test, $t_{11}=8.47$, $p < 10^{-4}$). The names of the two sites were then abbreviated to HV for the high-velocity site (Serrières-de-Briord) and to LV for the low-velocity site (Brégnier-Cordon). Bare sediments in the channels consisted mainly of medium sand for HV and fine sand for LV (Online Resource 1), following the Wentworth size classes (Wentworth 1922). The fine fraction of the bare sediments upstream of the vegetated patches, represented by the mean of the percentile value $d_{0.3}$ (see *Sediment characterization*), was significantly higher in HV than in LV in the period of sampling ($123 \pm 29 \mu\text{m}$ and $78 \pm 26 \mu\text{m}$, respectively; t-test, $t_{11}=-2.88$, $p < 0.01$).

The aquatic plant species *Callitriche platycarpa* was studied, as it is abundant in these channels and forms defined patches that are often well isolated (Fig. 1a). *C. platycarpa* is a heterophyllous species: submerged leaves are opposite, linear to narrowly oblanceolate, while apical ones are rhomboidal to obovate (Fig. 1b). At the shoot apex, leaves are densely packed, forming a rosette, which results 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 that can be 10-200cm long (Fig. 1c), forming dense patches due to the entanglement of stems (Tison and de Foucault 2014). Patches of *C. platycarpa* usually present an elliptical structure, and the patch height increases along the patch length. Long patches (usually over 1 m long) present an over-hanging canopy, created by the long, flexible and

buoyant stems extending in the downstream direction. Consequently, long patches are rooted only in the upstream part (Fig. 1a).



Fig. 1 Patch structure and morphology of *C. platycarpa*: (a) a long patch of *C. platycarpa*, with a typical elliptic shape and an overhanging canopy and only the upstream part of the patch being anchored to the sediment; (b) heterophylly in a plant of *C. platycarpa*, with linear/oblanceolate submerged leaves (bottom) and rhomboidal/obovate apical ones (top); (c) young plants of *C. platycarpa*, connected by a runner. Plants are highly branched and present an apex rosette

Field sampling

During summer 2014, six patches of *C. platycarpa* were selected at each site. The selected patches were located as far as possible from the channel banks and from other patches to avoid interference. The six patches per site were selected to have increasing length, between 0.16 m and 3.13 m for the LV site and between 0.3 m and 2.5 m for the HV site (Table 1). As patch length (L), width (W) and maximum height (h) were correlated (log-log relationship between L and W , $r = 0.84$, $p < 10^{-4}$, and linear relationship between L and h , $r = 0.83$, $p < 10^{-4}$), L was chosen to describe patch size. L/W , L/h and H/h ratios are reported in Table 1.

For each patch, coupled measurements of hydrodynamics and collection of sediment samples were performed at six sampling points along its longitudinal axis (two outside and four inside the patch). The two sampling points outside the patch were located approximately 1 m upstream from its leading edge (U) and 1 m downstream from its rear edge (D). The four sampling points inside the patch were located at 10%, 30%, 50%, and 90% of the canopy length, starting from the leading edge. For each position, the velocity profile was measured, and a core of sediment was collected (5 cm diameter and 10 cm deep).

Site	HV						LV					
Patch N.	1	2	3	4	5	6	1	2	3	4	5	6
L (m)	0.3	0.65	0.85	1.45	1.90	2.5	0.16	0.33	0.90	1.60	2.27	3.13
W (m)	0.1	0.19	0.55	1.00	0.84	0.6	0.08	0.16	0.50	0.40	0.80	0.70
h (m)	0.02	0.15	0.24	0.29	0.46	0.2	0.03	0.09	0.10	0.20	0.40	0.60
L/W	3	3.4	1.5	1.4	2.3	3.8	2	2.1	1.8	4	2.8	4.5
L/h	15	4.3	3.5	5	4.1	8.6	5.3	3.6	9	8	5.7	5.2
H (m)	0.4	0.57	0.56	0.89	0.86	0.5	0.48	0.69	0.68	0.65	0.51	0.62
H/h	27	3.8	2.3	3.1	1.9	1.9	16	7.7	6.8	3.2	1.3	1.0

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

Hydrodynamic measurements and velocity profiles

Vertical profiles of velocity were measured using a 3D Acoustic Doppler Velocimeter (ADV, FlowTracker Handheld-ADV, SonTek, USA). Vertical profiles were made with depth intervals of less than 12 cm, reduced to 1 - 4 cm near plant-water interfaces. Due to the dimensions of the side-looking probe, measurements closest to the sediment were taken at a minimum of 4 cm above the channel bed. Velocity was recorded over 100 s at 1 Hz. Data were filtered to remove spikes (Goring and Nikora 2002; Mori et al. 2007). The time average (denoted by an over bar) 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. This distance was chosen to avoid bottom interference due to the presence of boulders and cobbles. Moreover, this choice allowed us to measure hydrodynamic forces faced by plants during their growth and the patch development in relation to the patch architecture. Indeed, please note that 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 of depth were located above the canopy for the smallest patches and at the upstream end of long patches. In these cases, \bar{u}_{20} may qualitatively capture changes in the velocity field due to lateral deflection of flow away from the patch, but they will definitely over-estimate the velocity within the canopy. Turbulence intensity was not included in our study: for the smaller patches, velocity measurements within the patch were absent (for the reason mentioned above) and this impeded the detection of turbulence variation within the patch from the leading edge for different patch lengths.

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

Sediment characterization

After sampling, the collected sediment cores were stored at 4°C. To perform grain size analyses, sediments were wet sieved with distilled water at 1.6 mm 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). The analytical model used is based on the Fraunhofer theory, which assumes spherical particles. Prior to the measurements, sediments were sonicated for 2 min to destroy the aggregated 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 mode of the curve indicates the most abundant grain size in terms of the percentage per total solid volume. The curves were transformed into cumulative curves, and the percentile values $d_{0.1}$, $d_{0.3}$, $d_{0.5}$, were calculated (maximum diameter corresponding to 10%, 30%, and 50%, respectively, of the total particle volume). The three values were found to be correlated, and only the percentile value $d_{0.3}$ was kept for further analyses. Measurements of grain size were conducted in triplicate for each sample, and mean values and standard deviations of $d_{0.3}$ were calculated. To describe the sediment texture at each sampling position, we used only the mean value of $d_{0.3}$, as the standard deviation was less than 10%.

We expressed the $d_{0.3}$ relatively to the value measured at the upstream position ($d_{0.3 U}$) to obtain the relative value $\Delta d_{0.3}$ for each position, as $\Delta d_{0.3} = (d_{0.3} - d_{0.3 U}) \times (d_{0.3 U})^{-1}$. To assess whether the effect of patch length on sediment texture differs between the two sites, we calculated the relationship between $\Delta d_{0.3}$ at the 50% position and patch length using an exponential model ($\Delta d_{0.3} = a + b e^{-cL}$).

Results

Flow velocity

In terms of the \bar{u} profiles along the patch, the streamwise velocity profiles upstream of the patches generally followed a typical boundary layer profile, while at positions within the patches, \bar{u} decreased just above the canopy, usually reaching approximately zero within the canopy (Online Resource 2). Patches of the same length class studied at the two sites presented generally similar effects on velocity (\bar{u}_{20}) along the patch (Fig. 2a). For patches with $L \leq 0.65$ m, \bar{u}_{20} was generally unchanged from upstream to downstream because for these short patches, the

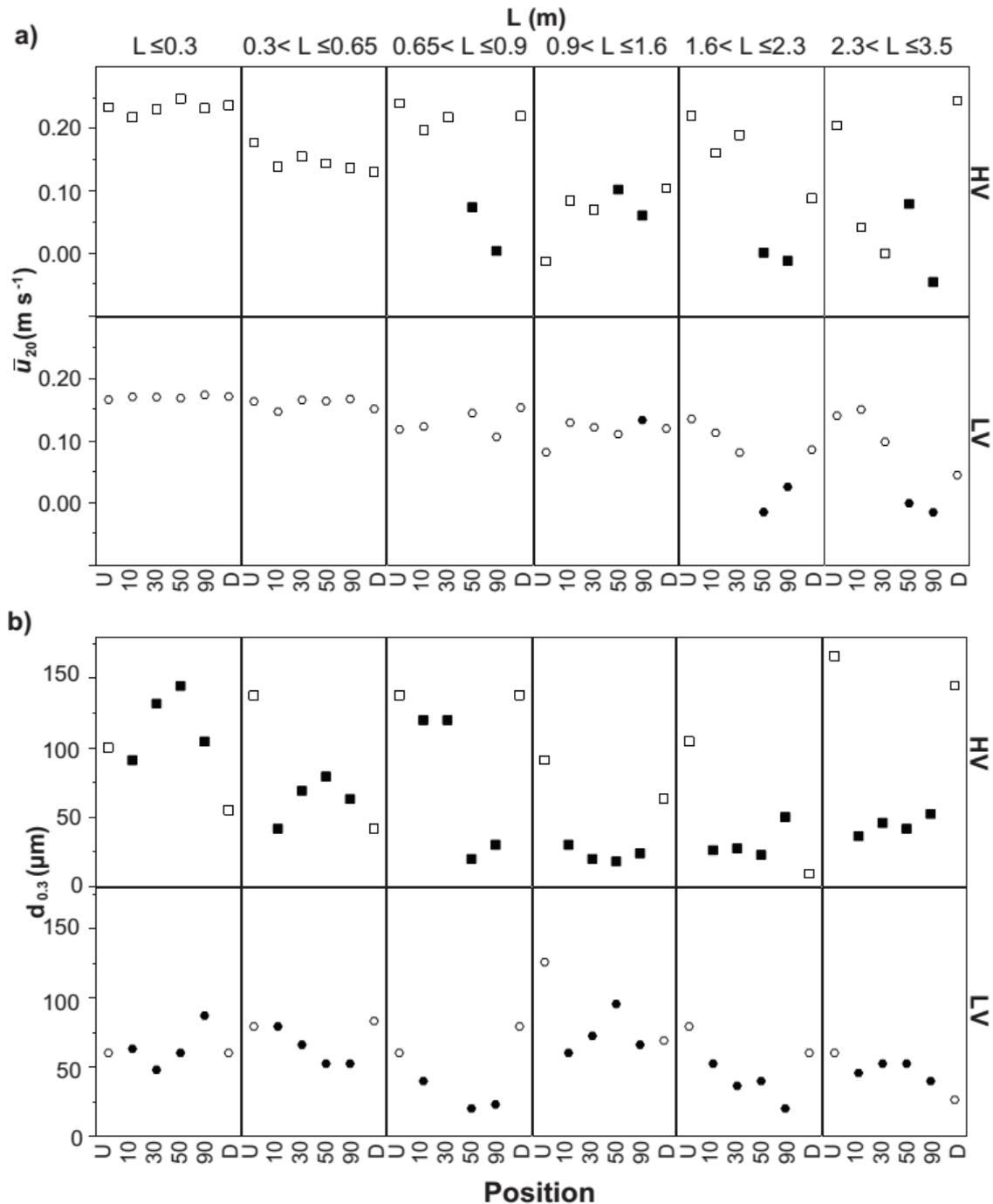


Fig. 2 (a) Time-averaged streamwise velocities, \bar{u}_{20} , and (b) the $d_{0.3}$ value in the grain size distribution measured at six positions for each patch: upstream (U), along the patch at 10%, 30%, 50% and 90% of its length, and downstream (D) along patches of the species *C. platycarpa* of increasing length (L) for the sites HV and LV. Empty symbols (squares for HV and circles for LV) indicate that the data refer to a position outside the patch canopy (either in the position U, D or when canopy was lower than 20 cm for \bar{u}_{20}), whereas full symbols indicate data collected inside the patch canopy.

measurement of \bar{u}_{20} was conducted above the canopy. For longer patches ($L > 0.65$ m), \bar{u}_{20} gradually decreased along patches that presented an overhanging canopy, with velocity close to zero or even negative observed at the 90% position in long patches (Fig. 2a).

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

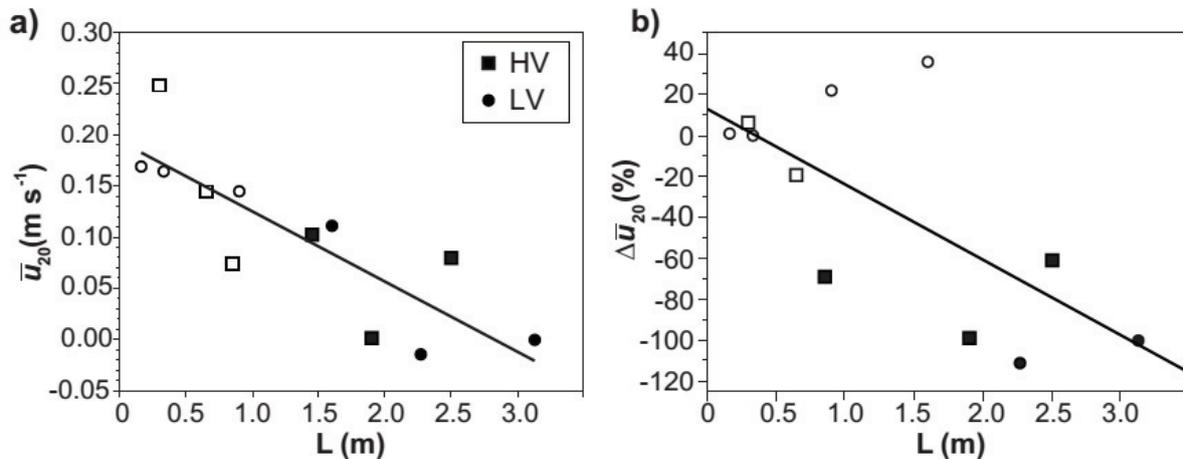


Fig. 3 Effect of patch length on velocity by the freshwater species *C. platycarpa* for the two sites. (a) \bar{u}_{20} at the 50% position was linearly negatively related to patch length ($F_{1,10} = 22.9$, $p < 0.001$), without significant differences between sites ($F_{2,9} = 0.02$, $p = 0.89$). (b) $\Delta\bar{u}_{20}$ at the 50% position was linearly negatively related to patch length ($F_{1,9} = 8.31$, $p < 0.02$), without significant differences between sites ($F_{2,8} = 1.45$, $p = 0.26$). Empty symbols (squares for HV and circles for LV) indicate that the canopy was lower than 20 cm for \bar{u}_{20} , whereas full symbols indicate data collected inside the patch canopy.

Sediment characteristics

For short patches ($L \leq 0.3$ m), $d_{0.3}$ within the patch was comparable to or larger than the upstream value, while for longer patches ($L > 0.3$ m), $d_{0.3}$ tended to be lower within the patch. The $d_{0.3}$ value generally decreased from upstream to downstream for patches of intermediate length ($0.3 < L \leq 0.9$ m), while for the longest patches ($L > 0.9$ m), the sediment texture generally did not vary along the patch, especially for positions 10%, 30%, and 50%, as a minimum value was reached at all positions (Fig. 2b). These results were in accordance with the cumulative grain size distributions collected along the central axis of patches (Online Resource 3): the cumulative distribution curves exhibited little variation in the short patches ($L \leq 0.3$ m), while for long patches ($L > 0.3$ m), the texture exhibited a higher volumic proportion of the fine fraction for the positions inside the patch (versus outside the patch). For these long patches, the volumic proportion generally increased from upstream to downstream for intermediately sized patches ($0.3 < L \leq 0.9$ m), while longer patches ($L > 0.9$ m) showed a more uniform grain size distribution (Online Resource 3).

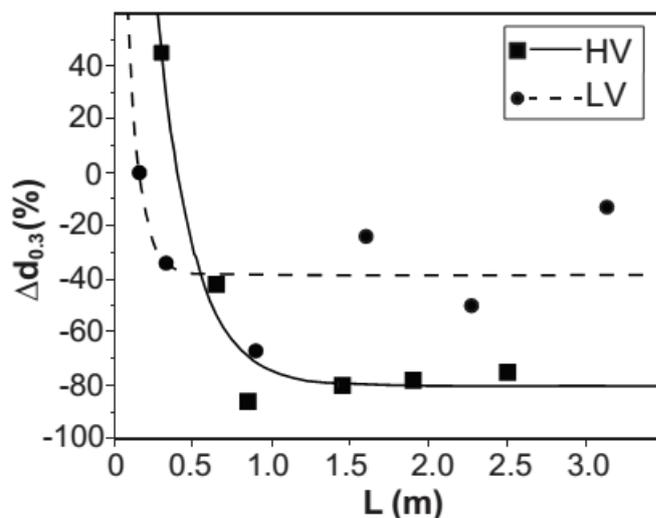


Fig. 4 Effect of patch length on sediment characteristics associated with the species *C. platycarpa* for the two sites. Δd_{30} at the 50% position exponentially decreased with patch length ($R^2 = 0.96$, $p < 0.05$ for HV and $R^2 = 0.40$, $p = 0.75$ for LV), and the relationship was different for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

The relationship between $\Delta d_{0.3}$ at the 50% position and patch length was different at the 2 sites. For the HV site, the $\Delta d_{0.3}$ exponentially decreased with patch length ($\Delta d_{0.3} = 4.71e$

$-4.39 L - 0.8$, $R^2 = 0.96$, $p < 0.05$): the $\Delta d_{0.3}$ decreased with patch length up to patches of 1.0 m, where it

reached a threshold value around -80% of $d_{0.3 U}$ (Fig. 4), corresponding to $d_{0.3} = 25 \mu\text{m}$ (data not shown). For the LV site, even though the relationship between $\Delta d_{0.3}$ and patch length was not significant ($\Delta d_{0.3} = 2.96 e^{-12.76 L} - 0.38$, $R^2 = 0.40$, $p = 0.75$, Fig. 4), the $\Delta d_{0.3}$ was reduced by between -13% and -67% of the $d_{0.3 U}$ for all the patches with $L > 0.3$ m, with a mean value of -38%, corresponding to $d_{0.3} = 52 \mu\text{m}$ (data not shown).

Effect of patch length on both sediment and flow

The relationship among relative velocity ($\Delta \bar{u}_{20}$), grain size distribution ($\Delta d_{0.3}$) and patch length can be summarized in a contour plot of the data relative to the 50% position, where the effect of the patch on flow velocity and sediment characteristics is expected to be maximal (Fig. 5). Small patches ($L < 1.1$ m) may present an increase in both $\Delta \bar{u}_{20}$ and $\Delta d_{0.3}$ (quadrant I of the plot), while for larger patches ($L > 1.1$ m), the increase in patch length generally results in reducing both $\Delta \bar{u}_{20}$ and $\Delta d_{0.3}$ (quadrant III of the plot).

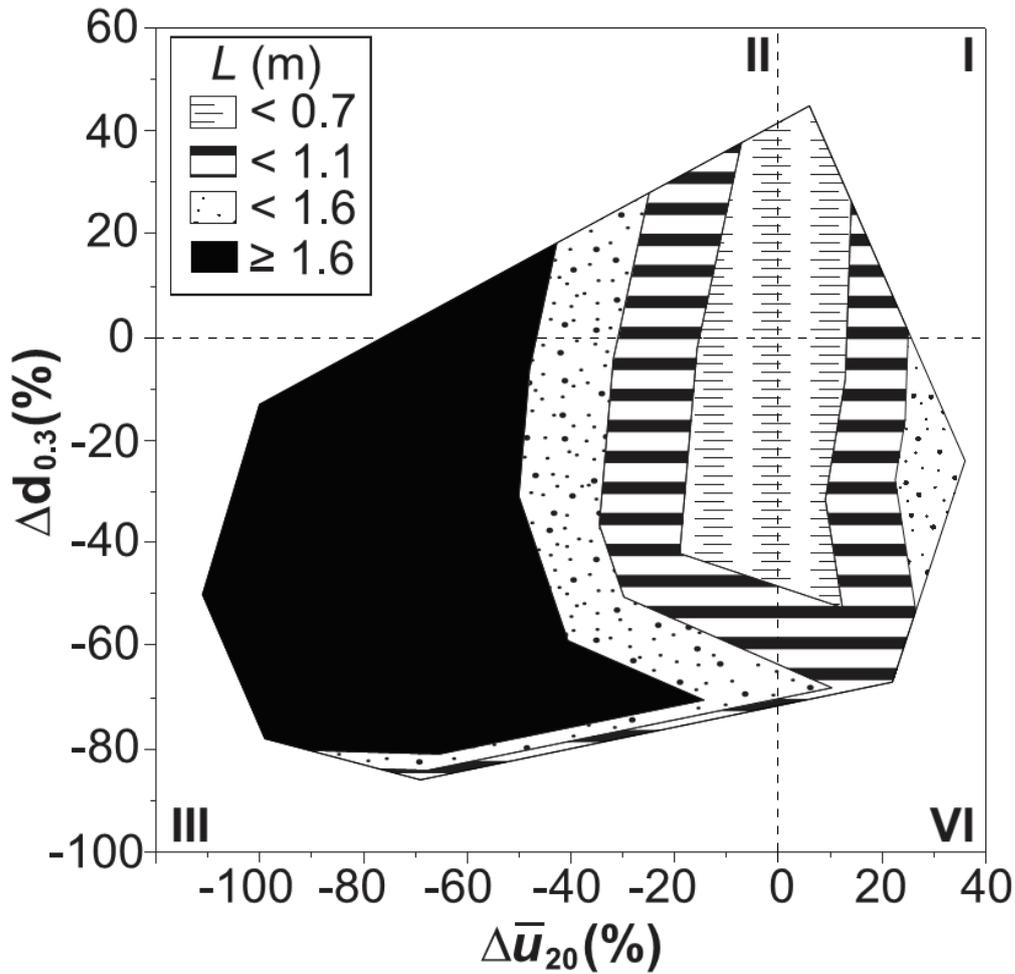


Fig. 5 Contour plot of the effect of patch length on both velocity ($\Delta \bar{u}_{20}$) and sediment texture ($\Delta d_{0.3}$) at both sites measured in the centre of the patches (50% position). The contour plot describes how the ecosystem engineer capacity of aquatic plant patches increases with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

Discussion

Patch structural characteristics are important factors that determine the capacity of a species to influence flow and sedimentation processes. The present study investigated the effects of patch size on these processes in order to test whether the effect of submerged plant patches on flow and sediment texture is dependent on patch size and whether this effect differs according to environmental conditions. Our results indicated that a minimal patch size is required to induce modifications of flow and sediment characteristics ($L > 0.65$ m and $L > 0.3$ m, respectively). Moreover, streamwise velocity decreased linearly with patch length independently of the site conditions. However, the sediment texture was dependent on site conditions: for the HV site, the $\Delta d_{0.3}$ in the middle of the patch exponentially decreased with patch length, reaching a minimum value at $L \geq 1.0$ m, while for the LV site, the $\Delta d_{0.3}$ decreased for all the patches with $L > 0.3$ m.

Effect of patch length on flow reduction

Our results demonstrate that submerged aquatic patches generally exhibited reduced in-patch velocity, as previously shown (Sand-Jensen 1998; Sand-Jensen and Pedersen 1999). In accordance with our first hypothesis, we demonstrated, for the first time, that modifications of velocity depend on patch size. The velocity near the patch was reduced to a greater degree by long patches, and for longer patches ($L \geq 0.65$ m), the velocity tended to be reduced from upstream to downstream to values close to 0 or even negative in the downstream part of the patch, which is consistent with previous results (Schoelynck et al. 2013). Negative values were associated with the vertical shear and recirculation generated in the wake of the patch, *e.g.*, details of which are illustrated in figure 2 of Folkard (2005).

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

The absence of an adjustment length (*i.e.*, an exponential reduction of the streamwise velocity up to a distance from the leading edge over which no further modification of flow is observable) in our data may indicate that the adjustment length was longer than the patch length in all cases due to the patch architecture of *C. platycarpa*, characterized by a very dense, flexible overhanging canopy and a positive correlation between patch height and length, which may lead to a different flow pattern than patches with different architecture (Chen et al. 2013). In addition, the positive relation between patch height and length implies that the submergence ratio (H/h) varies with patch length: small patches ($L \leq 0.3$) are deeply submerged ($H/h > 10$; Table 1) and, increasing patch length, H/h gradually decreases with longer patches becoming shallow submerged or even emergent (*i.e.* the canopy reaches the water surface, $H/h=1$; Table 1). The longest patches of *C. platycarpa* present also a gradual decrease of the ratio H/h from upstream to downstream, due to the flexibility and buoyancy of the canopy that is subjected to the drag exerted by the flow. As the H/h ratio controls the relative importance of the turbulent stress at the top of the canopy and the pressure gradient of the flow (Nepf 2012), the variation of H/h with patch length may consequently have an important role in flow and sedimentation patterns for different patch length that deserve to be further investigated.

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

The capacity of modifying the surrounding physical environment is a species-specific property that depends on plant traits (Bouma et al. 2010; Sand-Jensen and Pedersen 1999). Plant morphology and canopy architecture are important factors that determine the capacity of a species to modify flow characteristics (Fonseca and Fisher 1986; Sand-Jensen 1998; Schoelynck et al. 2014). A comparison of stiff and flexible species in salt marshes demonstrated how the stiff species was the most efficient ecosystem engineer, being able to attenuate the hydrodynamic forces with a slightly lower drag cost per unit biomass (Bouma et al. 2010). Future studies may focus on lotic species with contrasting canopy architecture and patch structure in order to test whether they present different patterns of flow reduction with increasing patch length.

Effect of patch length on sediment texture

As previously demonstrated, we observed the accumulation of fine sediment within plant patches (Sand-Jensen 1998; Schoelynck et al. 2013). In accordance with our first hypothesis, we demonstrated that the grain size within patches depends on patch size: small patches showed similar or coarser sediment compared to upstream conditions, and a minimum patch length was necessary for fine sediment accumulation that reduced the average grain size. At both sites, very short patches ($L \leq 0.3$ m) presented erosion or no effect on the sedimentation processes, as already observed in salt marsh environments for circular patches (Bouma et al. 2007). The increased grain size observed for short patches may be related to increased turbulence at the leading edge, which has been observed both in the field (Cotton et al. 2006) and in laboratory models (Zong and Nepf 2010; 2011). Above a minimal size ($L > 0.3$ m), finer sediment accumulation was observed. The reduction of velocity and turbulence within a patch favours the sedimentation of smaller particles (Hendriks et al. 2009; Liu and Nepf 2016; Sand-Jensen 1998; Schulz et al. 2003). In addition, suspended and bed-transported particles may be retained inside plant patches by collision with stems and leaves (Hendriks et al. 2008; Pluntke and Kozerski 2003). We demonstrated that the sediment texture distribution decreased exponentially as a function of patch length for the HV site, indicating that maximum sediment trapping was reached at a short length (approx. 1 m). For the LV site, even though the exponential relationship was not significant, the data suggest that the maximum sediment trapping potential was reached at $L = 0.33$ m.

In agreement with our first hypothesis, with increasing patch length, the accumulation of fine particles of sediment inside the patch increases up to a threshold length over which patches showed similar sediment texture distribution independently of patch length. This threshold length may correspond to the adjustment length, X_D (Chen et al. 2013), observed for artificial patches in flume experiments. X_D is the distance from the leading edge over which the velocity changes inside the patch, which is a function of patch stem density and height. Once the patch length exceeds X_D , the in-patch velocity does not decrease further with increasing length, and so the grain size does not change with further increases in patch length. In agreement with our second hypothesis, the two sites presented two different thresholds (1 and 0.33 m for HV and LV, respectively) and minimum $d_{0.3}$ values (25 and 52 μm for HV and LV, respectively). The difference in sediment texture ($d_{0.3}$ values) can be considered as a fingerprint of the suspended sediment available at the site: sites with lower values (HV) may have finer sediment in suspension and therefore require lower velocities to deposit all ranges of suspended particle sizes, including the finest ones. Very low flow velocities are found only

in long patches, and, therefore, the finest sediments are present only in the long patches (for HV, $L > 1.0$ m). Reciprocally, sites with a higher $d_{0.3}$ value (LV) may have suspended particles of larger dimension; in this case, even the finest range of particles available may also tend to deposit at higher near-bed velocities and therefore even in smaller patches (for LV, $L > 0.33$ m). The differences observed between the two sites may also be due to differences in plant morphology (e.g., stem density), leading to different adjustment lengths (Chen et al. 2013). In this case, a minimum velocity would be reached at different patch lengths, resulting in different sediment deposition patterns. The process of fine sediment accumulation within a patch may thus be influenced by both site conditions and plant and patch characteristics. Moreover, our finding may be influenced by the uniform condition of the sites in which the study was conducted: other sites with more variable conditions (e.g. channel structure, flow temporal variability) may present more complex flow and sedimentation patterns.

Effect of patch length on both sediment and flow

In accordance with our first hypothesis, we demonstrate that an increase in patch length generally results in a reduction in both $\Delta\bar{u}_{20}$ and $\Delta d_{0.3}$ for large patches ($L > 1.1$ m). For the small patches ($L < 1.1$ m), the majority of velocity measurements were conducted above the patch; in this case, values of $\Delta\bar{u}_{20} > 0$ describe the acceleration of flow above the canopy and over-estimate the in-patch velocity. In particular, the IV quadrant of Fig. 5, with $\Delta\bar{u}_{20} > 0$ and $\Delta d_{0.3} < 0$, describes a reduction in the sediment texture that should be related to a reduction in velocity inside the canopy that is not revealed by our measurements, as it occurs at a depth < 20 cm. Indeed, it is physically unlikely that the velocity within the patch was greater than the upstream velocity. However, it is clear that for shorter patches, the sediment texture was, in some cases, coarser than that under upstream conditions, and this modification of the sediment characteristics may be related to increased turbulence at the leading edge (Cotton et al. 2006; Zong and Nepf 2010; 2011).

In conclusion, this study demonstrated that sediment texture and hydrodynamics along patches are strongly dependent on patch length. In particular, a minimal patch size is required to significantly reduce velocity and accumulate fine sediment within plant patches, indicating that the ecosystem engineering effect of *C. platycarpa* is limited or even negative for small patches. A minimal patch size required to trigger the ecosystem engineering capacity of a species was already demonstrated for *S. alterniflora* in salt marsh environments: the habitat

modification induced by small patches is not sufficient to facilitate the establishment of other species in the patch, which is observed in longer patches (Bruno and Kennedy 2000). Similarly, we demonstrated that the engineering effect of *C. platycarpa* increases with increasing patch length, likely as a consequence of the increase in the quantity and volume of plants that intercept flow. The reduced velocity and increased sedimentation occurring within plant patches may lower the risk of plants suffering mechanical damage through the reduction of hydrodynamic forces (Sand-Jensen and Pedersen 2008; Schoelynck et al. 2012) and may increase nutrient availability due to the accumulation of fine sediment and associated nutrients, such as phosphorus (Sand-Jensen 1998). The effects of plant patches on flow and sediment characteristics may thus induce positive feedback for plants, favouring their growth and patch expansion. Future research must thus focus on the effect of patch length on nutrient accumulation and associated biogeochemical processes.

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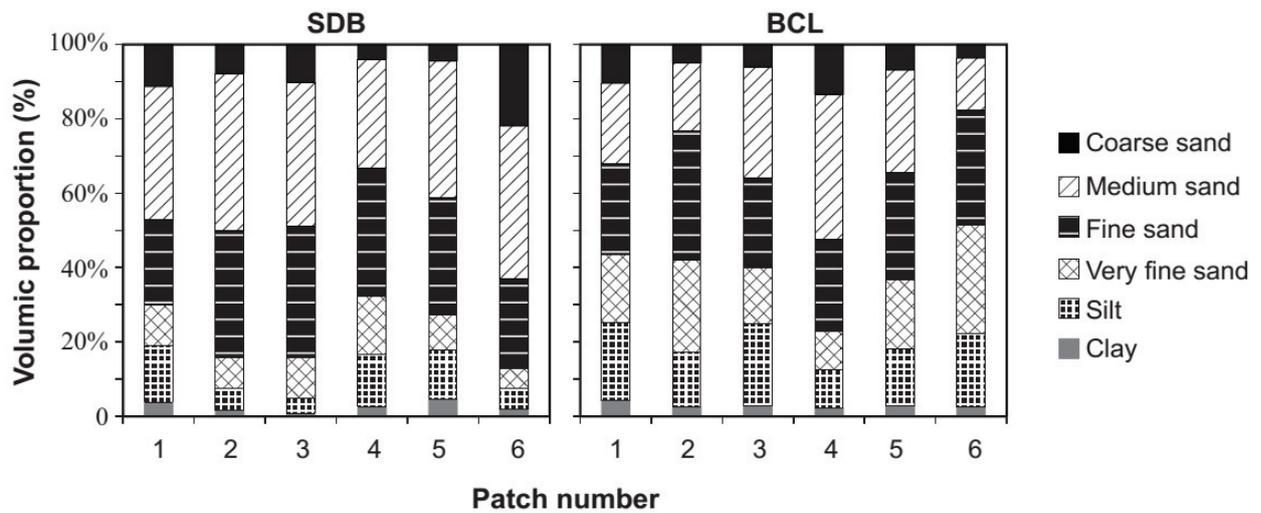
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Supplementary material captions

Online Resource 1

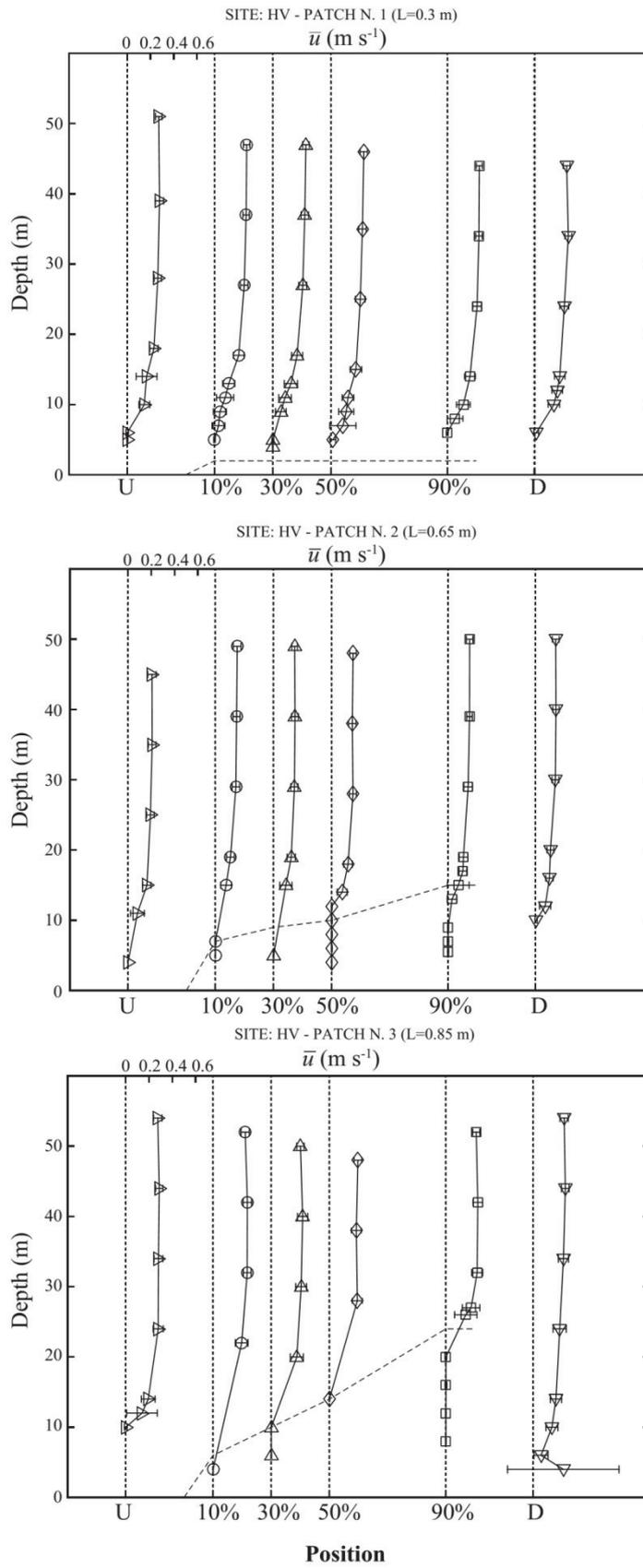
Sediment grain size distribution upstream of the patches of *C. platycarpa* at sites a) HV and b) LV. Patch number corresponds to a patch of increasing length (see Table 1). Sediment classification follows the Wentworth size classes (Wentworth 1922).



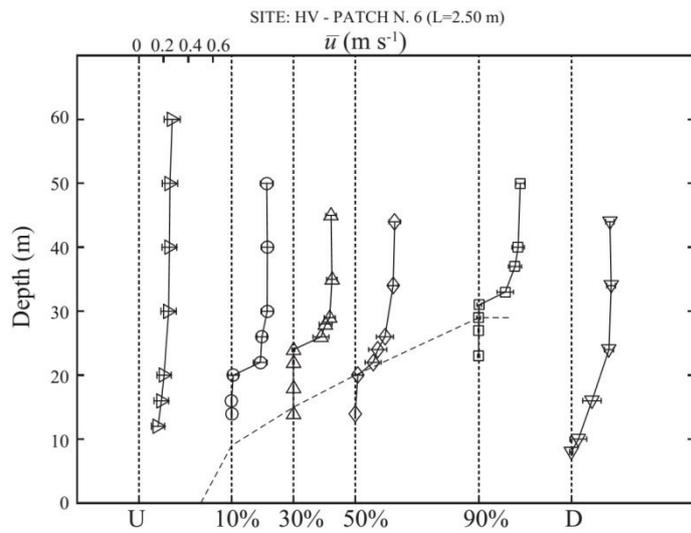
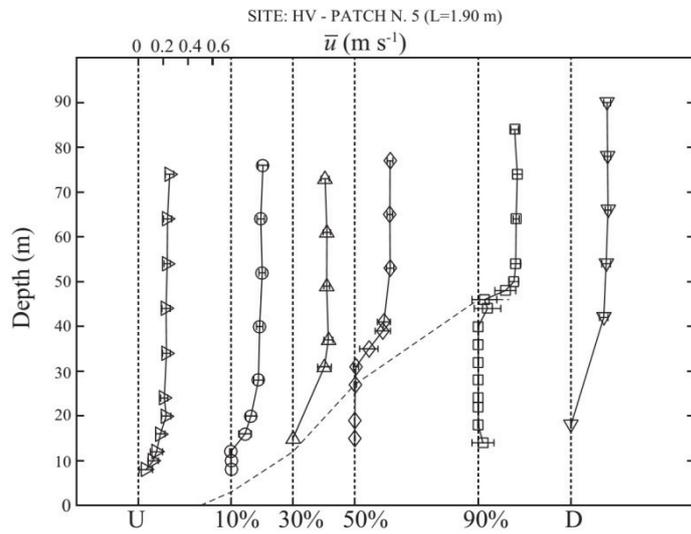
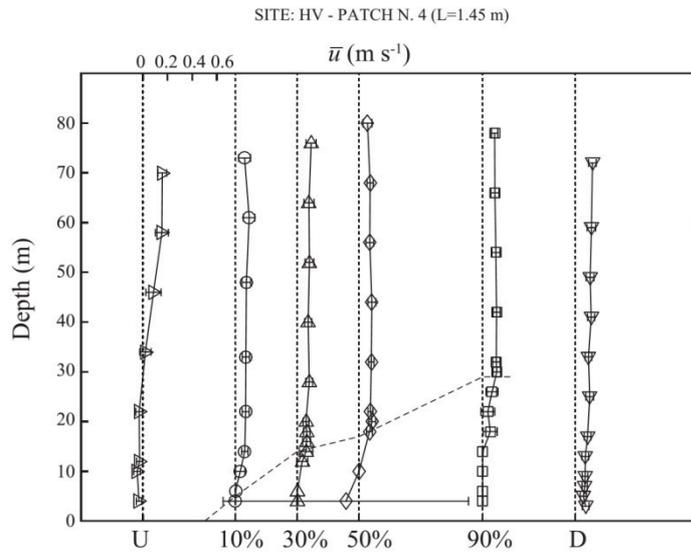
Online Resource 2

Time-averaged vertical profiles of streamwise velocity (\bar{u}) for patches of *C. platycarpa* of increasing size (see Table 1). Velocity profiles were sampled in six positions along the main axis of the patch: upstream (U, \triangleright), inside the patch at 10% (\circ), 30% (Δ), 50% (\diamond), and 90% (\square) of its length, and downstream (D, \triangledown). The dashed line indicates patch canopy height. (Continued on the following pages).

Online Resource 2

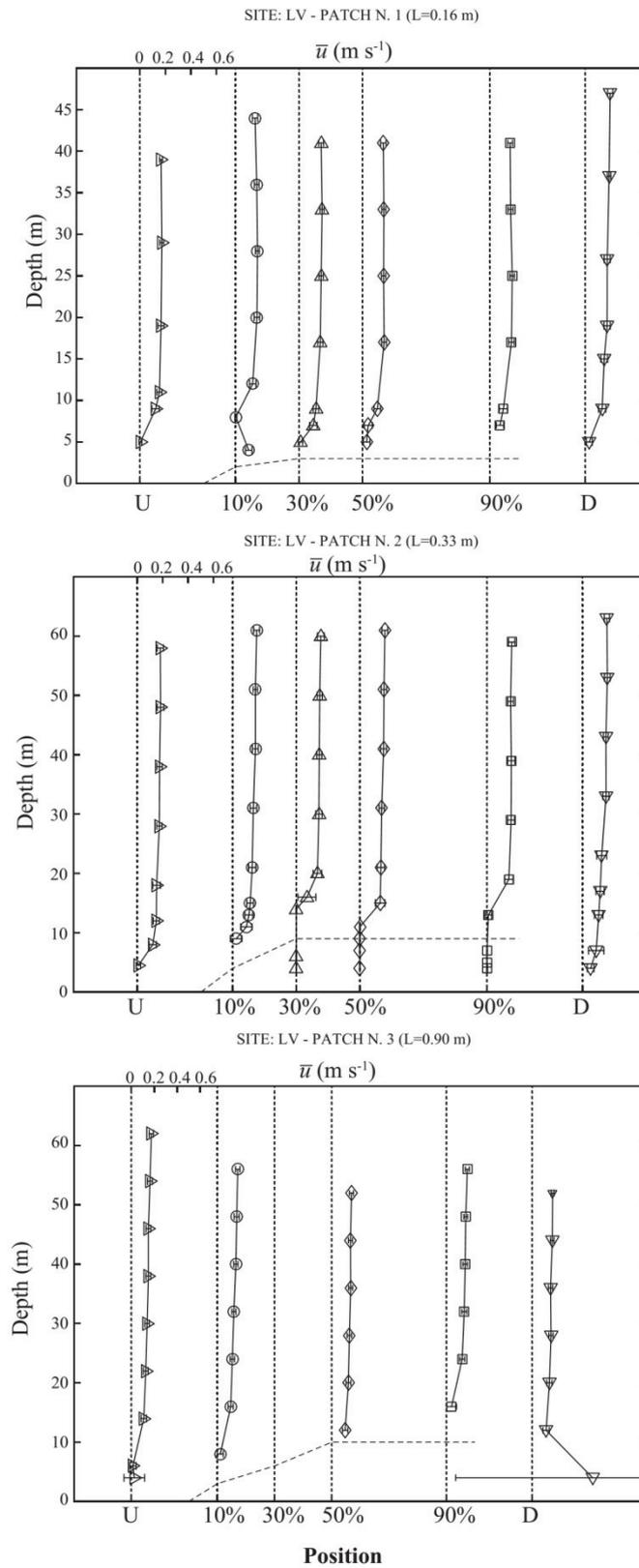


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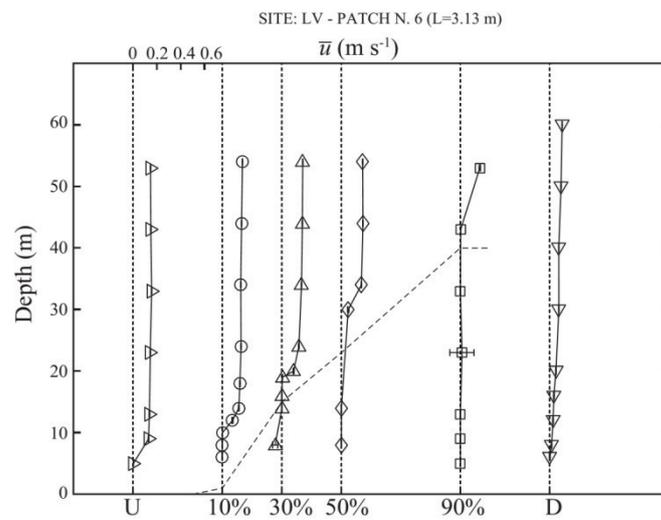
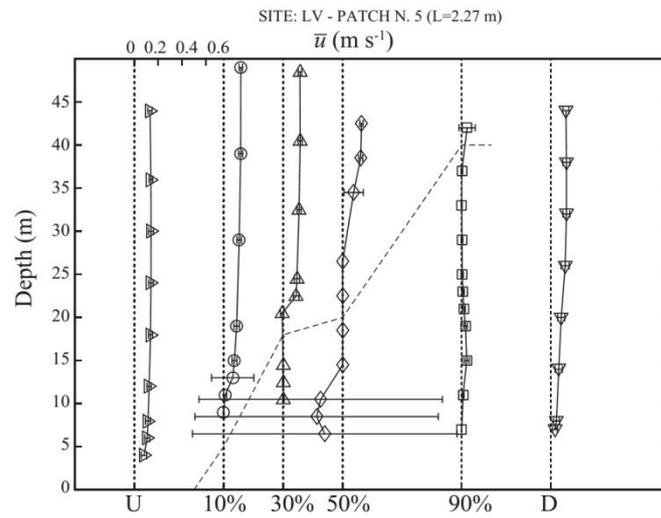
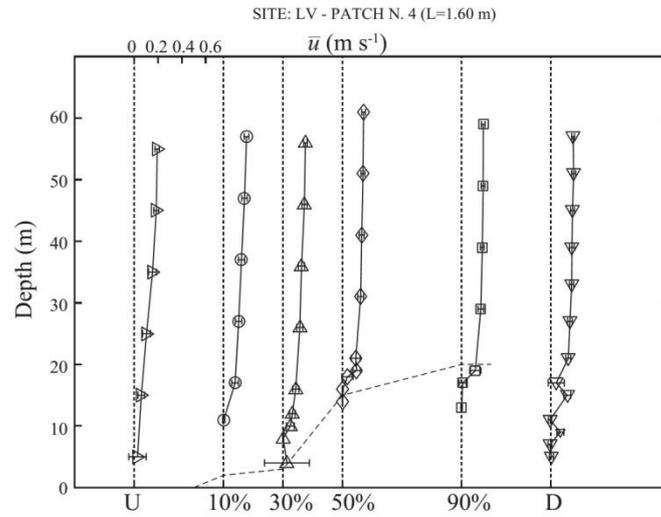


Position

Online Resource 2



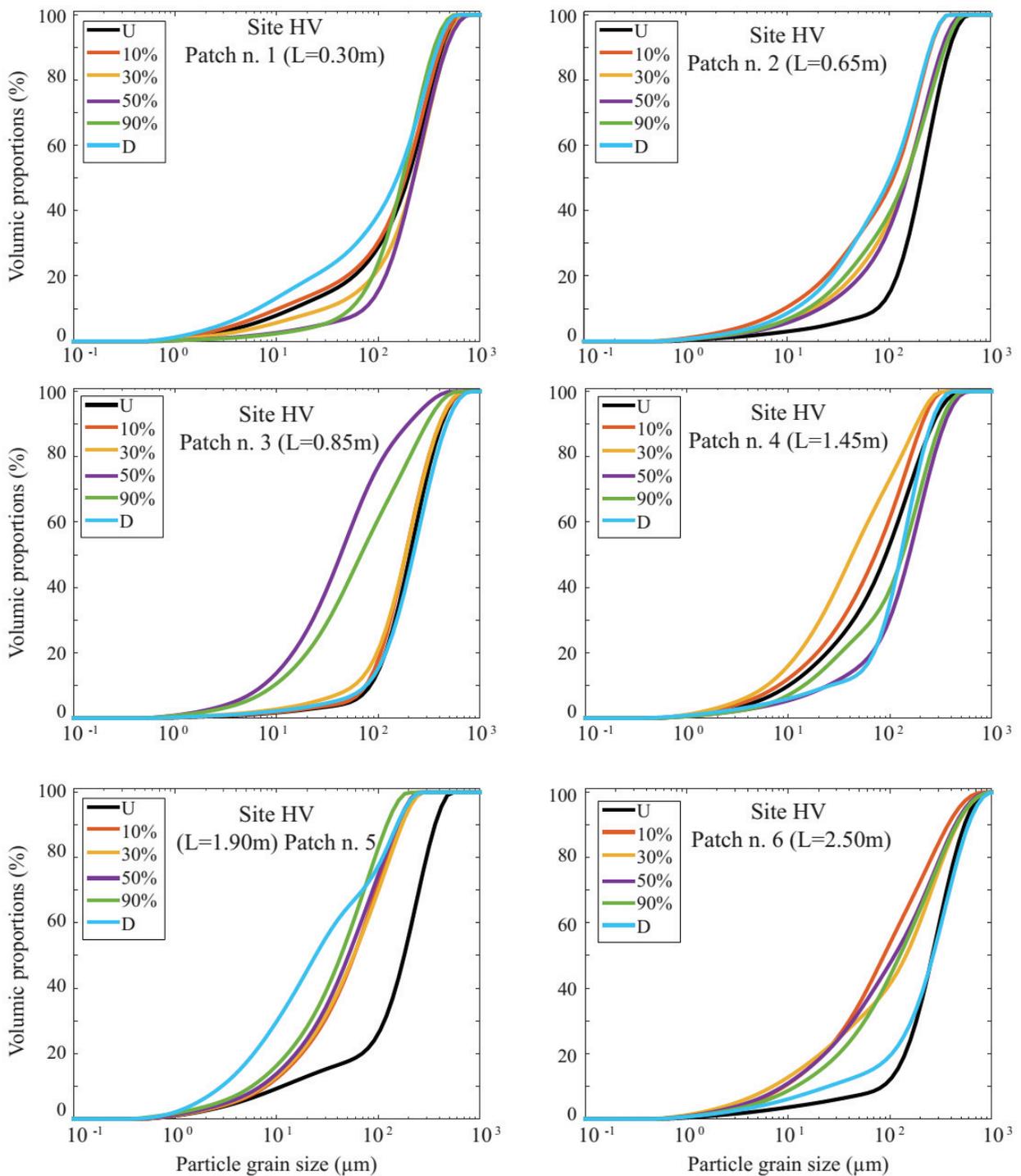
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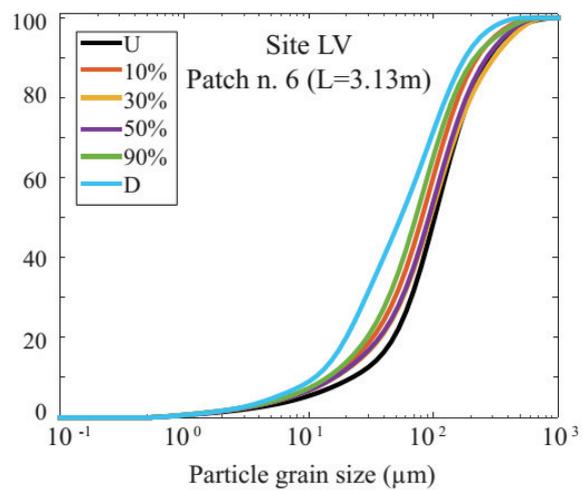
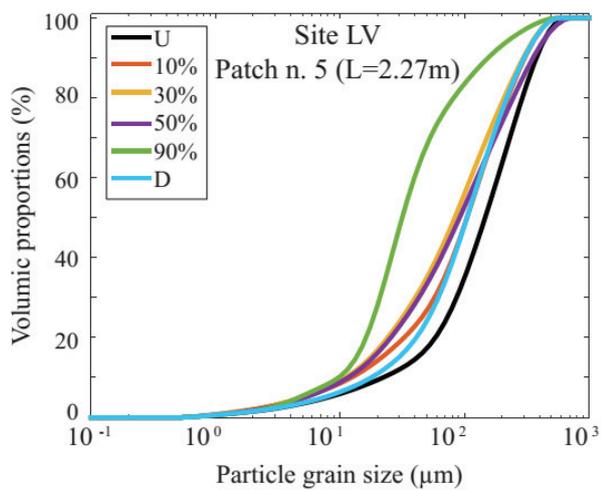
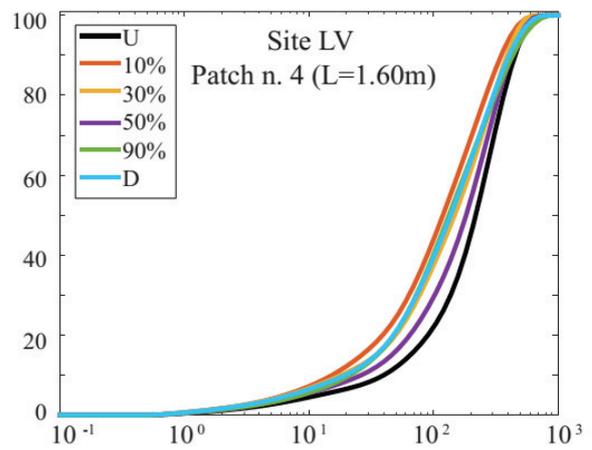
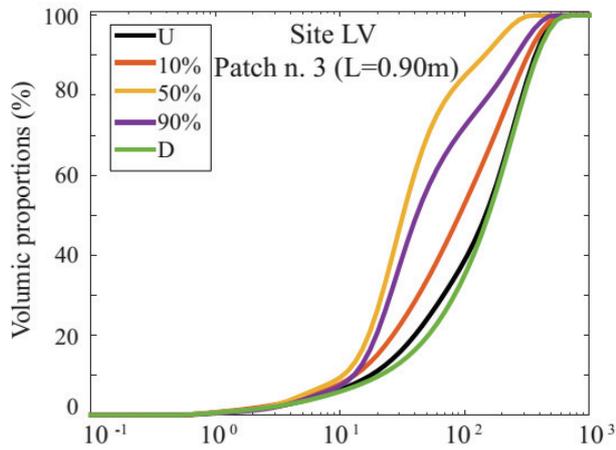
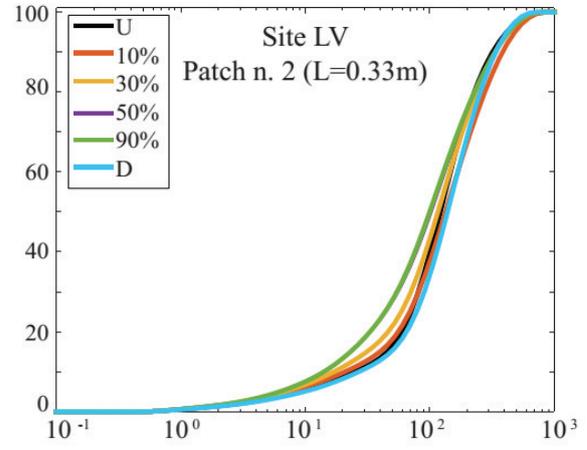
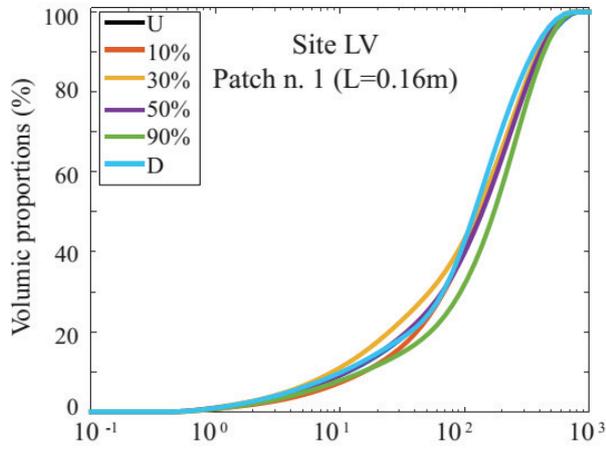
Position

Online Resource 3

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



Online Resource 3



CHAPTER 2

Effects of aquatic vegetation on hydrodynamics and biogeochemical processes

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Keywords: patch dynamics, patch size, ecosystem engineering, feedbacks, fitness, nutrient availability, biogeochemical processes, lotic environment.

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Abstract

In lotic ecosystems, scale dependent feedbacks resulting from physical habitat modifications control the lateral expansion of submerged plant patches, while the mechanisms that limit the patch expansion on a longitudinal dimension are still unknown. Our objective was to investigate the effects of patch length on the physical habitat modification, the consequences for the biogeochemical processes (i.e. accumulation/depletion of nutrient, microbial respiration) and the feedbacks (positive or negative) for the plant themselves. We measured flow velocity and sediment characteristics and microbial respiration rate, nutrient concentrations in interstitial water and plant height along natural patches of increasing length. These measurements were performed at two sites that differ in mean flow velocity, sediment grain size, and trophic level. Results showed a significant effect of patch length on organic matter content and nutrient concentrations in interstitial water. For short patches ($L < 0.9\text{m}$), all these parameters presented values close to the ones measured at the upstream position. For longer patches ($L \geq 0.9\text{m}$), within the patch organic matter content, orthophosphate and ammonium concentrations increased markedly compared to the upstream bare sediment, whereas nitrate concentrations decreased. Our results demonstrated an increased aerobic microbial activity and suggested that nitrification is inhibited while denitrification is enhanced within long patches. Finally, plant height was related to patch length by a quadratic pattern, indicating a maximum threshold length over which negative feedbacks occur, probably due to the high concentration of ammonium that in the concentration range measured may be toxic for plants. The threshold lengths over which patches influence the biogeochemical processes and negative feedbacks occur were reduced for increasing nutrient level in the ecosystem. We demonstrated that the plant-induced modifications of the physical habitat have cascading effects on the biogeochemical processes and plant growth, which depended on the environmental conditions, with consequences for patch dynamics and ecosystem functioning.

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; Hastings *et al.* 2007). The interaction between the ecosystem engineer and the environment may result in a 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). When feedbacks are positive at short distance and negative

at a long distance (i.e. scale-dependent feedbacks) the engineering may lead to the formation of regular patterns (or patchiness), even in homogeneous environmental conditions (Rietkerk and van de Koppel 2008). The long-distance negative feedback is fundamental for the formation of regular patterns, contrary to the short-distance positive feedback that, alone, is not a sufficient condition to create ecosystem patchiness (van de Koppel and Crain 2006; Rietkerk and van de Koppel 2008). Regular pattern formation generated through scale-dependent feedbacks has been observed in different environments for a wide range of organisms, as bushy vegetation in arid ecosystems (Klausmeier 1999; Barbier *et al.* 2006), shrubs and trees in nutrient-limited savannahs (Lejeune *et al.* 2002), tussock vegetation in freshwater intertidal wetlands (van de Koppel and Crain 2006), benthic diatoms in intertidal mudflats (Weerman *et al.* 2010) and, recently, for submerged aquatic vegetation in low-land rivers (Schoelynck *et al.* 2012).

In streams, aquatic submerged plants can form monospecific patches (Sand-Jensen and Madsen 1992). Patches are porous structures through which flow can partly pass, but with a reduced velocity, shear stress and turbulence relative to the upstream conditions (Sand-Jensen and Mebus 1996; Sand-Jensen and Pedersen 2008; Vandenbruwaene *et al.* 2011). Simultaneously, patches represent a region of high flow resistance, 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). As a result, inside plant patches the potential of 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), whereas flow acceleration next to the patch contributes to particle resuspension and erosion (Sand-Jensen 1998; Schoelynck *et al.* 2013). The plant-induced modifications of the physical environment trigger short-distance (i.e. inside the patch) positive feedbacks and long-distance (i.e. alongside the patch) negative feedback for the plants themselves (Schoelynck *et al.* 2012): inside patches, the reduced hydrodynamic stress results in reduced risk of mechanical damage (breakage, uprooting) and the sediment enriched in silt particles inside the patch, increases nitrogen and phosphorus concentrations (Chambers *et al.* 1992; Sand-Jensen 1998; Clarke and Wharton 2001; Sanders and Trimmer 2006), probably enhancing the nutrient availability for plants. In contrast, next to the patch, the coarser sediment that presents a lower concentration of nutrients (Chambers *et al.* 1992), may reduce plant growth. As a consequence, plant growth and thus patch expansion could be locally enhanced inside or immediately downstream a patch and inhibited

next to the patch leading to regular pattern formation (Sand-Jensen 1998; Schoelynck *et al.* 2012).

Beyond the feedbacks for the plants themselves, the modification of the physical environment induced by the ecosystem engineer may also have important implications for biogeochemical processes (Gutiérrez and Jones 2006). 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) and to sediment enrichment in organic matter and nutrients (Dahm *et al.* 1987; Sand-Jensen 1998; Schulz *et al.* 2003). As a consequence, the decomposition rate of organic matter could rise, resulting in enhanced sediment oxygen demand (Hargrave 1972), and in a reduced oxygen availability for microbial processes (Sanders *et al.* 2007), which itself may induce a shift from aerobic (e.g. nitrification) to anaerobic process (e.g. denitrification), (Gutiérrez and Jones 2006). Therefore, aquatic plants may also influence microbial processes, which in turn may regulate the nutrient availability for the plants.

Nutrient concentration induces a positive effect on aquatic plant growth (Gerloff and Krombholz 1966; Chambers and Kalff 1985; Duarte 1992), but at higher concentrations of sediment organic matter (Barko and Smart 1983; Sand-Jensen *et al.* 2005) and ammonium plant growth and photosynthesis can be inhibited (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) and lead to internal carbon-nitrogen imbalance (Cao *et al.* 2009). The ammonium concentration in the sediment is controlled by processes such as the accumulation of sediment and organic material, ammonification, nitrification and denitrification (Verstraete and Focht 1977; Ladd and Jackson 1982; Schmidt 1982; Seitzinger 1988; Wharton *et al.* 2006; Sanders *et al.* 2007). The regulation of these processes operated by the plants through physical ecosystem engineering may, therefore, be crucial for plant growth and survival.

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 modification increases with patch length (Bruno and Kennedy 2000; Bos *et al.* 2007). As the changes in biogeochemical processes are linked to the changes in physical conditions (Gutiérrez and

Jones 2006), the patch length should also influence the magnitude of changes in biogeochemical processes. Previous studies in lotic systems focused mainly 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 possible feedback for plants resulting from the biogeochemical processes on a streamwise dimension has never been investigated.

The objective of this work was to investigate the effects of patch length on biogeochemical processes (i.e. accumulation/depletion of nutriment, microbial respiration) in patchy ecosystems and the feedbacks (positive or negative) for the plant themselves arising from these effects. We addressed this question on plant patches in lotic ecosystems, where the permanent unidirectional flow influence sediment dynamics and related biogeochemical processes. First, considering that in-patch sediment characteristics may be driven by flow, we hypothesized that the effect of patches on within-patch sediment characteristics, proxies for the biogeochemical processes, along the patch, depends on patch size and increases for increasing patch length. We expect that flow and, consequently, sediment texture are reduced within the patch, and an increase of organic matter content in sediment is induced. In particular, we expect that short patches have limited or no accumulation of organic matter while the organic matter content of sediment increases for increasing position along the patch and for increasing patch length. As a consequence of organic matter accumulation patterns, we expect the orthophosphate and ammonium concentration in interstitial water to rise and nitrate concentration to fall with increasing patch length due to an establishment of anoxic conditions. We also expect that patch length has an effect on microbial activity through the regulation of the quantity and quality of organic matter in the sediment, with microbial respiration being unaffected in short patches but enhanced from upstream to downstream in long patches with a correspondent decrease in the quality of organic matter in sediment. Secondly, we hypothesize that plant height, a proxy for plant growth, depends on patch size and on plant position in the patch. In particular, we expect that, over a minimum patch length threshold, in the upstream part of the patch, plants height increases linearly with patch length, due to a positive feedback for plants. Instead, we expect that in the downstream part of the patch, the plant height has a quadratic pattern, increasing for increasing patch length up to a maximum length threshold over which the plant height decreases due to negative feedbacks induced by a high concentration of ammonium, as quadratic relation between plant growth and ammonium concentration were observed for some aquatic plant species (Clarke and

Baldwin 2002; Jampeetong and Brix 2009). Finally, we expect that the effect of patch length is dependent on site characteristics (i.e. trophic condition and sediment characteristics), with sites with different characteristics presenting different plant length thresholds that induce positive or negative feedbacks for plants.

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 rate of sediment, nutrient concentration in interstitial water and plant growth. Measurements were performed at two sites that differ 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) and Serrières-de-Briord (45.8153 N, 5.4269 E). These artificial drainage channels are fed by Rhône river seepage and hillslope aquifers. The channels were select because they present a simplified geomorphology (cross-section, water depth, low sinuosity) and reduced flow variability compared to natural channels while being colonized naturally by submerged aquatic vegetation. The type of channel feeding and their management keep the channel discharge relatively stable, especially in spring and summer season. The cover by aquatic vegetation ranges from 30 % to 90 % depending on the season and channel section.

The two sites presented slightly different daily average water velocities, sediment characteristics and nutrient concentrations. Depth-average and time-average velocities in the sampling days were higher in Serrières-de-Briord than in Brégnier-Cordon (Table 1). The names of the two sites were then abbreviated to HV for the high-velocity site (Serrières-de-Briord), and to LV for the low-velocity site (Brégnier-Cordon). Bare sediments in the channels consisted mainly of medium sand for HV site and fine sand for LV, following the Wentworth size classes (Wentworth 1922). The median and fine fraction of the bare sediments, respectively represented by the mean of the percentile values $d_{0.5}$ and $d_{0.3}$ (i.e. the maximal diameter of the 50% and 30% particle volume) was significantly higher in HV than in LV (Table 1), and the silt to clay ratio was lower in HV than in LV (Table 1). The site HV presented higher surface water concentration of orthophosphates and nitrates compared to the site LV (Table 1). The trophic status was poor for the site HV and moderate for the site LV

applying the Macrophyte Biological Index for Rivers, IBMR (Haury *et al.* 2006) during the spring-summer 2014 (Table 1).

The aquatic plant species *Callitriche platycarpa* Kütz. was studied, as it is abundant in these channels and it forms defined patches that are often well isolated. *C. platycarpa* has densely packed leaves, forming a rosette at the shoot apex, and resulting in a large part of the biomass 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 due to the entanglement of stems (Tison and de Foucault 2014). Patches of *C. platycarpa* usually present an elliptical structure and the patch height increases along the patch length. Patches over 1m long usually present an over-hanging canopy, created by the long, flexible and buoyant stems extending in the downstream direction. Consequently, patches over 1m long are rooted only in the upstream part. Patches of *C. platycarpa* can reach a maximal length around 3.0- 3.5m. Exceptional lengths of 4.5-4.7 m have been observed, but are probably due to the uprooting of a part of the canopy and its temporarily entanglement to the rest of the canopy which is still rooted (S. Licci, personal observation).

SITE	LV	HV	t -test		
			t value	df	p
Z_{Ch} (m)	0.8	1.3			
W_{Ch} (m)	6.0	8.0			
U (ms⁻¹)	0.13 ± 0.01	0.20 ± 0.01	8.47	10	<10⁻⁴
d_{0.5} (µm)	165 ± 46.2	231 ± 41.1	-2.59	10	<0.05
d_{0.3} (µm)	78 ± 26	123 ± 29	-2.88	10	<0.05
Silt/Clay	6.16 ± 1.47	4.02 ± 1.08	2.88	10	<0.05
Λ (µS cm⁻¹)	374 ± 2	447 ± 2	28.96	28	<10⁻⁴
T(°C)	13.7±0.3	14.4±0.3	1.58	28	0.12
pH	8.1±0.2	8.3±0.2	0.88	28	0.38
PO₄³⁻ (ppb)	37.4±11.0	53.1±10.6	3.96	28	<10⁻³
NH₄⁺ (ppb)	19.3±3.5	22.3±3.5	0.59	26	0.56
NO₃⁻ (ppm)	3.6±0.9	11.05±12.65	18.9	28	<10⁻⁴
IBMR (trophic level)	10.51 (moderate)	9.55 (poor)			

Table 1. Description of the two sites studied: channel geomorphology (maximum channel depth (Z_{Ch}) and width (W_{Ch})); depth-averaged and time-averaged velocity (U); sediment characteristics (fine fraction expressed as percentile value ($d_{0.3}$) and the silt to clay ratio); surface water physico-chemical characteristics (conductivity (Λ), temperature (T), pH, concentration of orthophosphate (PO_4^{3-}), ammonium (NH_4^+) and nitrate (NO_3^-)); trophic level (Macrophyte Biological Index for Rivers (IBMR), Haury *et al.* 2006). Differences in flow velocity, sediment characteristics and surface water physico-chemical characteristics between sites have been tested with a t-test.

2.2 Field sampling

During summer 2014, five patches of *C. platycarpa* were selected in each site. Selected patches were located as far as possible from the channel banks and from other patches to avoid interferences. The five patches per site were selected of increasing length, between 0.16 m and 3.13 m for the LV site and between 0.30 m and 2.50 m for the HV site, covering the full range of observed lengths in the two sites. Patch length (L), width (W) and maximal height (h) were measured with a tape measure. As W and h were correlated to L (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.

For each patch, water velocity measurements, sediment and interstitial water sample collection were performed at five sampling points along its longitudinal axis (one outside and four inside plant patch). The sampling point outside the patch was located approximately 1m

upstream from its leading edge (U) and was taken as a reference to the local condition near the patch. The four sampling points inside the patch were located at 10%, 30%, 50%, and 90% of canopy length, starting from the leading edge. For each position, water velocity profile measurements were first performed, then a sample of interstitial water followed by a core of sediment were collected. Finally, plants were harvested at the 10% and at the 90% of canopy length.

2.3 Hydrodynamic measurements

Vertical profiles of velocity were measured using a 3D Acoustic Doppler Velocimeter (ADV, FlowTracker Handheld-ADV, SonTek, USA). Vertical profiles were made with depth intervals of less than 12 cm, 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 us to measure hydrodynamic forces faced by plants during their growth and the patch development in relation to the patch architecture. Indeed, please note that 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 of depth were located above the canopy for the shortest patches and at the upstream end of long patches. In these cases, \bar{u}_{20} may qualitatively capture changes in the velocity field due to lateral deflection of flow away from the patch, but they will definitely over-estimate the velocity within the canopy.

To examine the effect of a plant patch on flow 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, $\bar{u}_{20\text{ U}}$. That is, for the 50% position, we defined $\Delta\bar{u}_{20} = (\bar{u}_{20} - \bar{u}_{20\text{ U}}) \times (\bar{u}_{20\text{ U}})^{-1}$.

2.4 Sediment characterization

Sediment texture

At each sampling position, sediment was sampled manually using clear Perspex cores (5cm diameter and 10cm deep). After sampling, the collected sediment samples were stored in a cool box with ice during the sampling day and then placed at 4°C in a laboratory refrigerator. 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 macro-aggregated 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 $d_{0.1}$, $d_{0.3}$, $d_{0.5}$, were calculated (maximum diameter corresponding to 10%, 30%, and 50%, respectively, of the total particle volume). The three values were found to be correlated, and only the percentile value $d_{0.3}$ was kept for further analyses. The $d_{0.3}$ allows characterising the sediment fine fraction (very fine sand, silt and clay) in our sites. Measurements of grain size were conducted in triplicate for each sample, and mean values and standard deviations of $d_{0.3}$ were calculated. To describe the sediment texture at each sampling position, we used only the mean value of $d_{0.3}$, as the standard deviation was less than 10%. We expressed the $d_{0.3}$ relatively to the value measured at the upstream position ($d_{0.3 U}$) to obtain the relative value $\Delta d_{0.3}$ for the 50% position only, as $\Delta d_{0.3} = (d_{0.3} - d_{0.3 U}) \times (d_{0.3 U})^{-1}$.

Sediment organic matter content and interstitial water chemical characteristics

Organic matter content (OM) was measured for each sediment sample by weight loss after ignition at 550°C for 2 hours (LOI, Dean 1974). Measurements of organic matter content were done in triplicate for each 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%. The arithmetic mean value of the organic matter content and its standard deviation for the different positions in each patch was calculated to investigate the effect of patch length on the whole patch.

Interstitial water was sampled with a 60 ml syringe and screened mini-piezometers (1m long, 1.7cm diameter, and 5cm screen length) pushed 20cm deep inside the sediments using an internal metallic rod (Dahm *et al.* 1996; Lefebvre *et al.* 2005). 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. Interstitial water chemical characteristics were analyzed within 48 hours, based on standard colorimetric methods, measuring 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), using an automatic analyzer (Easychem Plus; Systea, Anagni, Italy). The arithmetic mean value of orthophosphate, ammonium and nitrate concentrations and their standard deviation for the different positions in each patch was calculated to investigate the effect of patch length on the whole patch.

Finally; for each sampling position, the sum of ammonium, nitrate and nitrite concentration was used to obtain the total inorganic nitrogen concentration in interstitial water (TN). Then, the relative concentration of the nitrogen forms (ammonium, nitrite, and nitrate) in interstitial water was calculated for each plant patch position.

Microbial respiration rate

Within 24 hours from sediment collection, three subsamples of 5ml of fresh sediment collected from the surface of each core. The sub-samples were incubated to measure the potential sediment microbial respiration rate ($\mu\text{g} (\text{O}_2) \text{h}^{-1} \text{g}_{\text{dry sed}}^{-1}$). Sediment sub-samples were incubated in bottles of 125ml sealed by a double cap and filled with surface water from the river collected at the same time previously saturated in oxygen and placed under controlled conditions (15°C, dark, and stirring to avoid O_2 depletion) for 15h ca. For each subsample, the oxygen consumption was calculated by measuring O_2 concentration at the beginning and at the end of the incubation by optical dissolved oxygen sensor (HQ40D; Hach, Loveland, CO, USA). To measure the exact dry weight of each subsample each subsample was transferred to a previously weighed aluminium cup once the incubation was finished and then dried at 70°C until constant weight was reached. For each sampling site, microbial respiration rate measurements were effectuated only for a short patch ($L < 0.5 \text{ m}$) and a long patch ($2.27\text{m} \leq L \leq 2.50\text{m}$).

Carbon to nitrogen ratio

For the same samples used for measuring microbial respiration rate we also measured the C:N ratio in, to assess the quality of the organic matter content in the sediment. For each sediment sample analyzed, two sub-samples were finely ground, acidified with HCl (2mol l⁻¹) and then placed in ultra-light-weight silver capsules to measure the total nitrogen and total carbon by elemental analyzer (FlashEA; Thermo Fisher Scientific, Waltham, MA, USA). Then, the mean C:N content of bare and within-patch sediment was calculated. For each sampling site, C:N analyses were performed for one short patch (L<0.5m) and one long patch (2.27≤L≤2.50 m).

2.5 Plant morphology

Five specimens of plants were harvested at the 10% and at the 90% of canopy length. Plants were stored in sealed plastic bags saturated with water in a climatically-controlled room at 19°C for a maximum 48h until they were analyzed. For each plant sampled, we measured plant height (H) with a ruler and its mean value was calculated from measurements at two different positions in the patch: upstream of the patch (10% of patch length) and downstream of the patch (90% of patch length). Plant height was used as a proxy for plant growth and is recognized as a functional trait indicating the response to hydrodynamic stress and nutrient resources in the bed sediment which together affect biogeochemical cycles (Lavorel *et al.* 2007).

2.6 Statistical analyses

To test the effects of patch length and position within the patch on sediment organic matter content, nutrient concentrations (i.e. orthophosphates, ammonium, and nitrates) and the relative concentration of nitrogen forms in interstitial water, we used the non-parametric Friedman test, due to the small number of patch lengths (n=5) and positions for patch (n=4). The Dunnett's test was used to compare the parameter values of within-patch position with the upstream position (multicomparison with control, Dunnett 1955; Dunnett 1964).

The Kruskal-Wallis test was used to test differences in microbial respiration rate between positions in a short and a long patch from the two river sites. If the null hypothesis of the Kruskal-Wallis test was rejected, the Dunnett's test with control was used to compare the upstream respiration rate (i.e. the control) with the respiration rate measured inside the patch. The Quade test (Quade 1979) was used to compare the microbial respiration rate in different positions between short and long patches for the two sites. The Quade test is a non-parametric two-way analysis of variance, and it was chosen as it is useful for testing small samples and

treatments that have a great difference in variability (Quade 1979). The Student's t-test was used to compare the C:N content of bare and within-patch sediment of a short and a long patch for the two sites.

Finally, linear and quadratic models were fitted to the plant height data measured at the 10% and 90% position for the full range of patches of increasing length (n=5). The Quade test was used to compare the mean plant height at 10% and 90% position for the full range of patches of different length (n=5).

For all the tests, the significance level was 0.05.

3. Results

3.1 Hydrodynamics measurements

At the two river sites, plant patches with comparable lengths presented generally similar effects on velocity (\bar{u}_{20}) in the middle of the patch. For short patches ($L \leq 0.65$ m), \bar{u}_{20} was generally unchanged or accelerated ($\Delta\bar{u}_{20} \geq 0$) because for these short patches, the measurement of \bar{u}_{20} was conducted above the canopy (Table 2). 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 2).

3.2 Sediment characterization

Sediment texture

At the two sites, for the shortest patches ($L \leq 0.3$ m), $d_{0.3}$ within the patch was comparable to or larger than the upstream value ($\Delta d_{0.3} \geq 0$), while for longer patches ($L > 0.3$ m), $d_{0.3}$ within the patch tended to be lower than the upstream value ($\Delta d_{0.3} < 0$; Table 2). For the LV site, the $\Delta d_{0.3}$ was reduced by between -13% and -67% of the $d_{0.3}$ measured at the upstream position for all the patches with $L > 0.3$ m (Table 2). For the HV site, the $\Delta d_{0.3}$ decreased with patch length up to patches of 0.85 m, where it reached a threshold value fluctuating around -80% of the $d_{0.3}$ measured at the upstream position (Table 2).

SITE	L (m)	\bar{u}_{20} (ms ⁻¹)	$\Delta\bar{u}_{20}$	d _{0.3} (μ m)	$\Delta d_{0.3}$
LV	0.16	0.17	0.01	60.26	0.00
	0.33	0.16	0.00	52.48	-0.34
	0.90	0.14	0.22	19.95	-0.67
	2.27	<0.01	-1.11	39.81	-0.50
	3.13	<0.01	-1.00	52.48	-0.13
HV	0.30	0.25	0.06	144.86	0.44
	0.65	0.14	-0.19	79.43	-0.42
	0.85	0.07	-0.69	19.95	-0.86
	1.90	<0.01	-0.99	22.91	-0.78
	2.50	0.08	-0.61	41.78	-0.75

Table 2. Water velocity (\bar{u}_{20}) and sediment texture(d_{0.3}) measured in the middle of patches of *C. platycarpa* with increasing length in the two sites (LV, HV). Values are reported in the table both as absolute values (\bar{u}_{20} , d_{0.3}) and as values relative to the value measured at the upstream position ($\Delta\bar{u}_{20}$, $\Delta d_{0.3}$).

SITE	LV			HV		
	Mean	Range	CV (%)	Mean	Range	CV (%)
OM (%)	1.94	1.12 - 2.93	20.9	0.93	0.69-1.27	0.21
PO ₄ ³⁻ (ppb)	698	71.69 - 3716	212	86.8	31.1 – 145	48.4
NH ₄ ⁺ (ppb)	528	22.4 - 2102	150	328	84.7 - 762	78.7
NO ₃ ⁻ (ppm)	2.38	0.23 - 4.50	70	3.17	0.14 – 13.3	160
NH ₄ ⁺ / TN (%)	0.21	0.00 - 0.88	154	0.24	0.02 – 0.38	65.2
NO ₃ ⁻ / TN (%)	0.77	0.10 - 0.98	43.7	0.73	0.57 - 0.98	24.0
NO ₂ ⁻ / TN (%)	0.01	0.01 - 0.02	42.3	0.02	0.00 – 0.06	82.2

Table 3. Summary statistics (mean, range, and coefficient of variation) regarding the sediment characteristics (organic matter content (OM); interstitial water concentrations of orthophosphates (PO₄³⁻), ammonium (NH₄⁺), nitrates (NO₃⁻); relative concentrations of the total nitrogen forms (TN) in interstitial water (NH₄⁺ / TN, NO₃⁻ / TN, NO₂⁻ / TN)) of the bare sediment sampled upstream of the patches investigated for the two sites investigated (LV, HV).

Sediment organic matter content and interstitial water characteristics

For the site LV, patch length had a significant effect on organic matter content in sediment, nutrient concentrations in interstitial water and on ammonium and nitrate concentrations relative to the total nitrogen content (TN) (Fig. 1; Table 4). For short patches ($L < 0.9\text{m}$), all these parameters presented values close to the ones measured at the upstream position (Fig. 1 a-e; Tables 3, 4). For longer patches ($L \geq 0.9\text{m}$), organic matter content in the sediment, orthophosphate and ammonium concentrations increased markedly compared to the upstream bare sediment whereas nitrate concentration decreased within the patch (Fig. 1a-d; Tables 3, 4). Nitrate went from being the predominant form of nitrogen (95%-100% of total nitrogen) within short patches ($L < 0.9\text{m}$) to being surpassed by ammonium (60-95% of total nitrogen) within long patches ($L \geq 0.9\text{m}$; Fig. 1e; Table 4). NO_2^- relative concentrations were negligible for all patches (Fig. 1e). In contrast, the effect of the position within the patch on sediment organic matter content, nutrient concentrations in the interstitial water, and the relative concentration of ammonium and nitrates, were not significant (Fig. 1; Table 5).

For the site HV, the effects of patch length and position on the sediment organic matter content were not significant due to the non-monotonous variation of this parameter that often presented a maximum value in the middle of each patch (Fig. 2a; Tables 4, 5). With the exception of the shortest patch ($L = 0.30\text{ m}$), all patches with lengths $\geq 0.65\text{m}$ the organic matter content increased for nearly all positions inside the patch compared to the upstream position (Fig. 2a). The organic matter did not increase at the 10% position in certain patches maybe due to stem related turbulence at the upstream edge of the patch, which usually increases the fine sediment resuspension depleting the organic matter in sediment. However, the effect of patch length on the concentration of orthophosphate, ammonium and nitrate in interstitial water was significant (Table 4). For all the patches investigated, orthophosphate and ammonium concentrations in interstitial water were higher inside the patches compared to the upstream concentration whereas nitrate concentration was lower (Fig. 2b-d; Table 3, 4). The effect of the sampling position was significant for orthophosphate and ammonium concentration in interstitial water, but not for the nitrate concentration (Table 5).

There was no significant effect of patch length on ammonium and nitrate concentrations relative to the total nitrogen content (Fig. 2e; Table 4). Compared to the LV site, the reduction of the relative concentration of nitrate was already apparent in the two shortest patches (Fig. 2e). The effect of the sampling position inside the patch on the relative concentrations of ammonium and nitrate was significant (Fig. 2e; Table 5). The relative concentration of ammonium tended to increase whereas the relative concentration of nitrate

tended to decrease along the patch from upstream to downstream, while nitrites were present in low relative concentration whatever the position (Fig. 2e).

Site	Factor: <u>LENGTH</u> parameter	Friedman test		
		chi ²	df	p
LV	OM	12.4	4	0.01 *
	PO ₄ ³⁻	14.2	4	<0.01 **
	NH ₄ ⁺	14.0	4	<0.01 **
	NO ₃ ⁻	13.3	4	<0.01 **
	%NH ₄ ⁺ /TN	12.8	4	0.01*
	%NO ₃ ⁻ /TN	12.8	4	0.01*
	HV	OM	9.4	4
PO ₄ ³⁻		16.0	4	0.003 **
NH ₄ ⁺		13.4	4	<0.01 **
NO ₃ ⁻		13.0	4	0.01*
%NH ₄ ⁺ /TN		7.0	4	0.14
%NO ₃ ⁻ /TN		7.0	4	0.14

Table 4. Effect of patch length on organic matter content of sediment and on nutrient concentrations in interstitial water tested with a Friedman test.

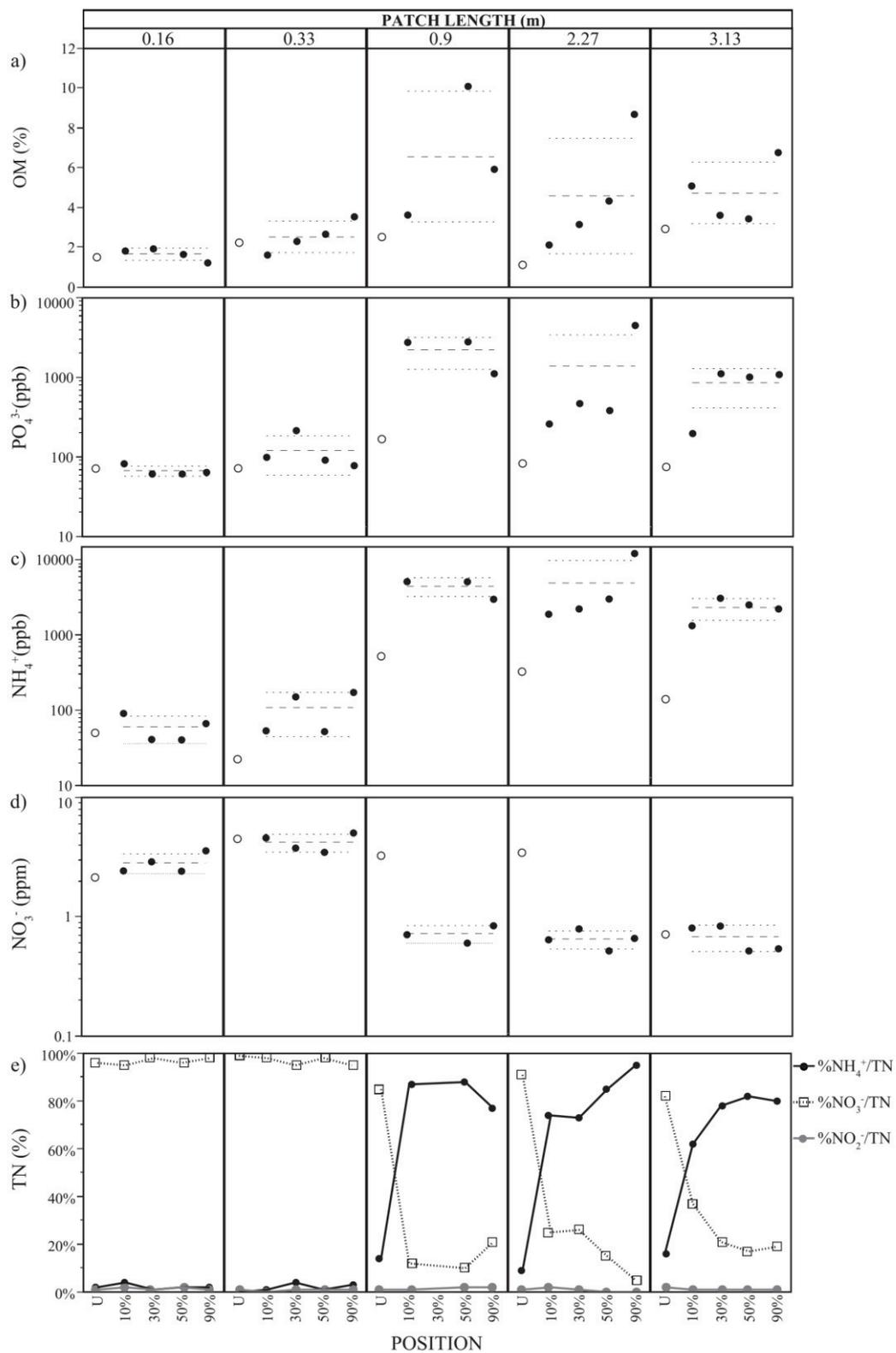


Fig. 1. (Continued on the following page).

Fig. 1. Organic matter content of sediment (a), nutrient concentration in interstitial water (orthophosphates, b, ammonium, c, nitrate, d) and relatives forms of nitrogen (e) along the patches of increasing length of *Callitriche platycarpa* in the site LV. Sampling positions were located 1 m upstream the patch (U) and within the patch at 10%, 30%, 50%, and 90% of canopy length. Full dots indicate the parameter values measured for sediment within the patches, while empty dots indicate the parameter values measured for the bare sediment at the upstream position (control). Dashed and dotted lines indicate respectively mean and standard deviation of in-patch values. .

Factor:		Friedman test			Dunnett's test - multicomparison with control (U versus positions inside the patch) - p-value			
<u>POSITION</u>								
Site	parameter	chi²	df	p	10%	30%	50%	90%
LV	OM	8.2	4	0.08				
	PO₄³⁻	5.8	4	0.21				
	NH₄⁺	7.5	4	0.11				
	NO₃⁻	8.5	4	0.08				
	%NH₄⁺/TN	5.9	4	0.20				
	%NO₃⁻/TN	5.9	4	0.20				
HV	OM	7.5	4	0.11				
	PO₄³⁻	12.5	4	0.01 *	p<0.01	p<0.01	p<0.05	p<0.05
	NH₄⁺	10.1	4	0.04 *	ns	p<0.05	p<0.05	p<0.05
	NO₃⁻	4.2	4	0.38				
	%NH₄⁺/TN	11.5	4	0.02 *	ns	p<0.01	p<0.05	p<0.01
	%NO₃⁻/TN	11.5	4	0.02 *	ns	p<0.01	p<0.05	p<0.01

Table 5. Effect of position along the patch on organic matter content of sediment and nutrient concentrations in interstitial water for patches of increasing length (Friedman test). When the effect of position resulted significant, the difference of each in-patch position from the upstream position were tested by Dunnett's test.

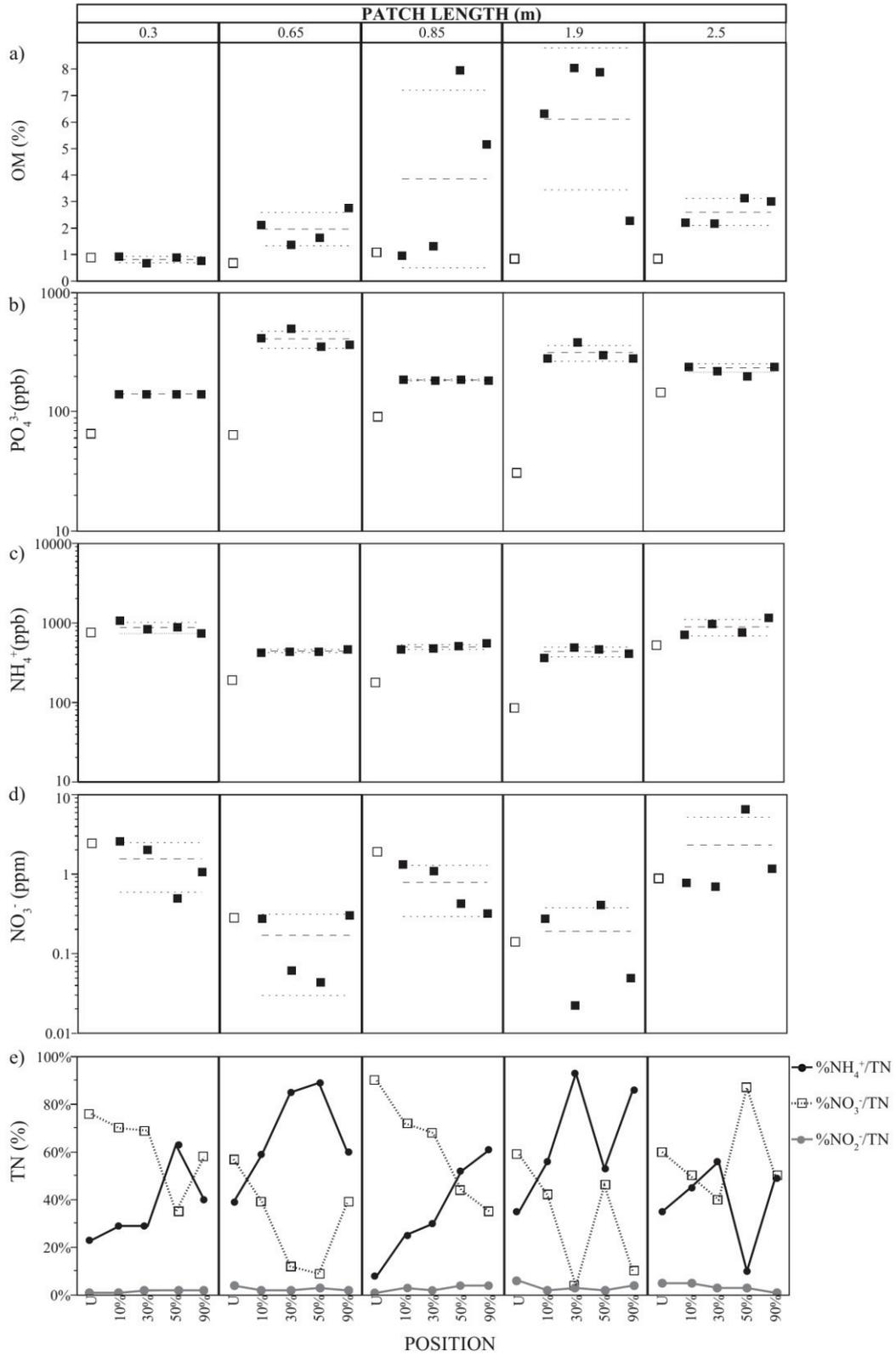


Fig. 2. (Continued on the following page).

Fig.2. Organic matter content of sediment (a), nutrient concentration in interstitial water (orthophosphates, b, ammonium, c, nitrate, d) and relatives forms of nitrogen (e) along the patches of increasing length of *Callitriche platycarpa* in the site HV. Sampling positions are explained in the legend of Fig. 1. Full squares indicate the parameter values measured for sediment within the patches, while empty squares indicate the parameter values measured for the bare sediment at the upstream position (control). Dashed and dotted lines indicate respectively mean and standard deviation of in-patch values.

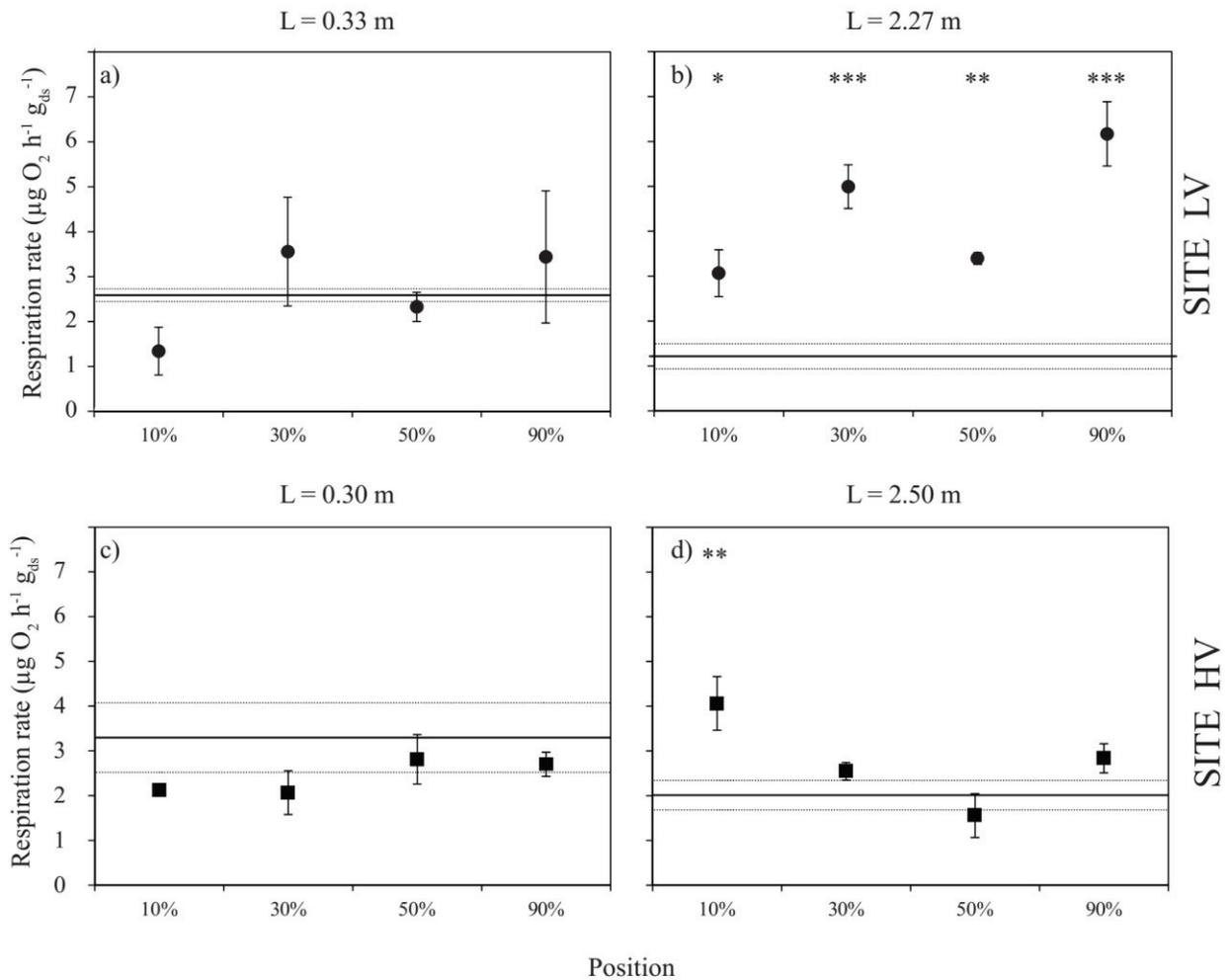


Fig. 3. Microbial respiration rate along a short patch (L = 0.3 to 0.33 m) and a long patch (L = 2.27 to 2.50 m) for the two sites, LV and HV. Circles for LV and squares (or HV represent the mean value while error bars represent standard deviation of microbial respiration rate for subsamples (n=3) of sediment collected in different patch positions. Sampling positions are explained in the legend of Fig. 1. The horizontal lines indicate the mean and the standard deviation of the sediment respiration rate for the bare sediment upstream of the patch. Significant differences from the mean upstream value are indicated by asterisks (Dunnett's test with control, *: p < 0.01; **: p < 0.001; ***: p < 0.0001).

Effect of patch length on microbial respiration

For both sites, the respiration rate of sediment measured in short patches (L=0.30m and L=0.33m for LV and HV, respectively) did not significantly differ between positions along the patch and did not differ from the respiration rate measured for the bare sediment upstream of the patch (Fig. 3a, c, Kruskal-Wallis test, $\chi^2_4=7.56$, $p=0.11$ and $\chi^2_4=8.43$, $p=0.08$ for sites LV and HV, respectively). In contrast, for long patches (L=2.27m) in the LV site, the respiration rate increased from upstream to downstream (Fig. 3b; Kruskal-Wallis test, $\chi^2_4=12.78$, $p=0.012$), with all the respiration rate measured inside the patch being significantly higher than the upstream respiration rate (Dunnett's test with control, Fig. 3b). For a long patch (L=2.50m) in the site HV, the microbial respiration rate was significantly higher only at the 10% position compared to the upstream value (Fig. 3d; Kruskal-Wallis test, $\chi^2_4=12.50$, $p=0.014$; Dunnett's test with control), while for the other positions inside the patch the respiration rate measured was not significantly different compared to the upstream respiration rate (Fig. 3d).

The sediment respiration rate for different positions inside the patch was significantly higher for the long patch than for the short patch only in the site LV (Quade test, $F_{(1,3)} = 15$; $p < 0.05$), while it did not significantly differ for the two patches of different lengths in the site HV (Quade test, $F_{(1,3)} = 0.46$; $p = 0.54$).

Effect of patch length on sediment C:N

For both sites, the mean C:N of sediment did not significantly differ between short patches and the bare sediment (Table 6). In contrast, for the long patches, the mean value of C:N tended to increase in the sediment inside the patch compared to the bare sediment upstream of the patch, but this difference was only significant for the LV site (Table 6).

3.3 Effect of patch length on plant height

For the site LV, the mean plant height (H) sampled at the 10% position was not linearly related to patch length ($R^2 = 0.71$, $p = 0.07$) but followed a quadratic pattern (Fig. 4a; $R^2 = 0.99$, $p < 0.001$) with a maximum height reached for L=1.8 m. Similarly, at the 90% position (downstream part of the patch), plant height for increasing patch length followed a quadratic pattern (Fig. 4b; $R^2=0.98$, $p < 0.01$), with a comparable maximum value for L of 1.8m. Plant height did not differ between the 10% and 90% positions for a patch of increasing length (Quade test, $F_{(1,4)}=0.015$, $p=0.91$), and the maximum plant height was reached for the same length (1.8m).

For the site HV, plant height at the 10% position did not vary with increasing patch length (Fig. 4c; $R^2 = 0.15$, $p = 0.52$). At the 90% position, plant height was not related by a quadratic model to patch length (Fig. 4d; $R^2 = 0.55$, $p = 0.36$). The plants positioned at 90% of the patch length are significantly longer than the plants collected at the 10% position (Fig 4 c, d; Quade test, $F_{(1,4)} = 18$, $p = 0.013$).

Site	L (m)	Sediment type	Mean C:N \pm S.D	t-test (t, p, df)
LV	0.33	Bare	9.74 ± 0.24	1.01, 0.38, 3
		In-patch	9.17 ± 0.50	
	2.27	Bare	7.38 ± 0.06	-3.26, <0.05, 3
		In-patch	10.89 ± 0.96	
HV	0.30	Bare	8.69 ± 0.31	0.89, 0.47, 2
		In-patch	7.53 ± 1.13	
	2.50	Bare	$8.69 \pm 0.31^{\S}$	-1.94, 0.15, 3
		In-patch	19.69 ± 5.07	

Table 6. Comparison of C:N characteristics of sediment in bare sediment and in vegetated sediment for patches of different length (t-test). [§] The value of C:N of bare sediment in a short patch is used as a reference for the value of the bare sediment in a long patch.

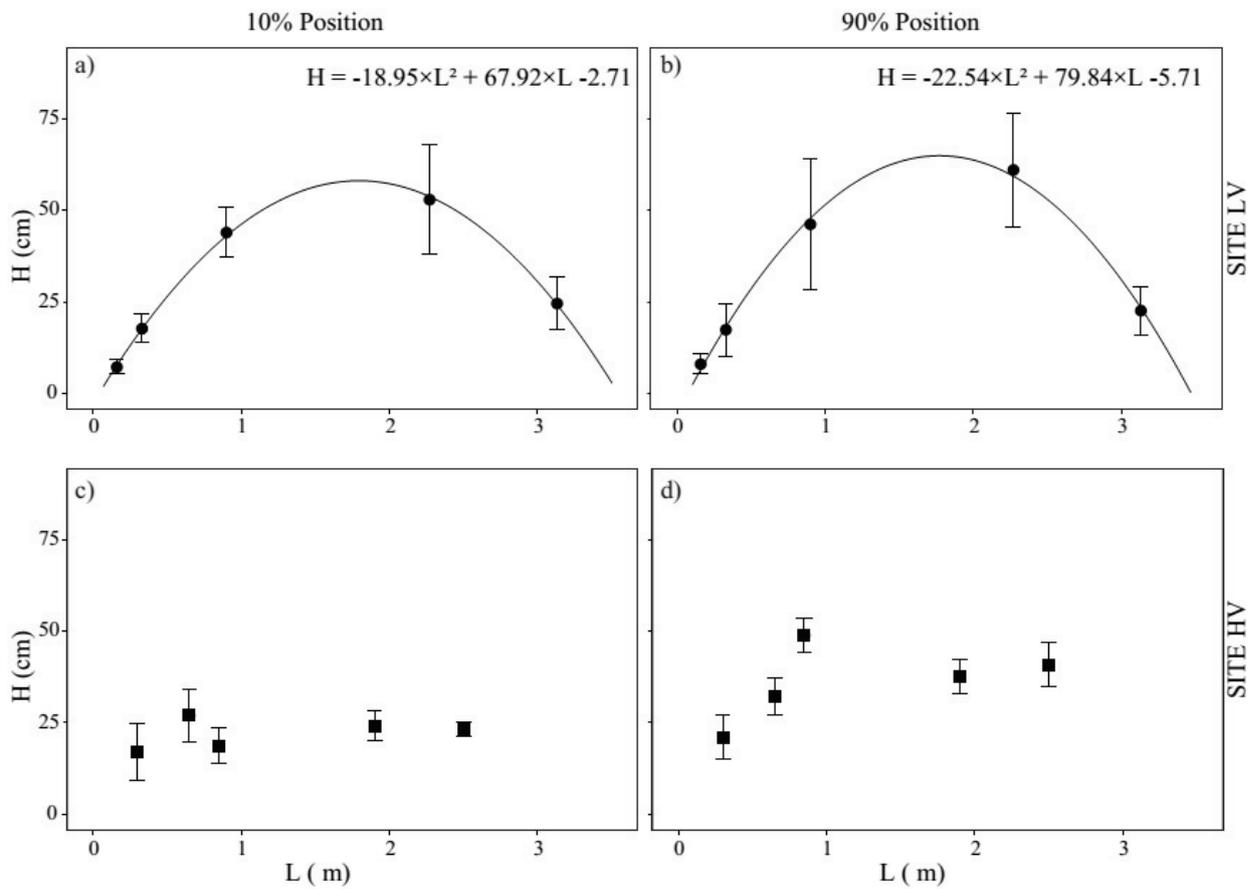


Fig. 4. Effect of patch length (L) and position (10% and 90%) on plant height (H), a proxy for plant growth, along patches of *Callitriche platycarpa*, for the site LV at the 10% (a) and 90%(b) position and for the site HV at the 10% (c) and 90%(d). Circles for LV and squares for HV represent the mean value while error bars represent standard deviation of plant height for specimens (n=5) collected in patches of increasing length.

4. Discussion

The present study investigated the effects of patch length and of position within the patch on hydrodynamics and sediment characteristics, proxies for the biogeochemical processes, and the presence of length thresholds that may induce positive or negative feedbacks for plant patches. Our results demonstrated that patch length, through its effects on hydrodynamics, regulates the biogeochemical processes. Our findings also indicate that different nutrient conditions compared to the bare sediment exist in patches above certain length thresholds and that these thresholds seem to be associated with positive or negative feedbacks

4.1 Effect of patch length on hydrodynamic and sediment texture

In accordance with our first hypothesis, our results demonstrated that flow velocity and sediment texture both depended on patch length. For both sites, the shortest patches ($L \leq 0.30\text{m}$), showed no change or an increase of both flow velocity and sediment texture indicating that the patch had a little or negative influence on velocity and sediment at the measured depth. Even if, for certain intermediate patches, $\Delta \bar{u}_{20}$ had positive values, describing the acceleration of flow above the canopy and over-estimating the in-patch velocity, the in-patch velocity for patches with $L > 0.30\text{m}$ was certainly reduced, as confirmed by the sediment texture ($d_{0.3}$) that was always reduced in these patches.

4.2 Effect of patch length on sediment biogeochemical processes

For both sites, in accordance with our first hypothesis, we demonstrated, for the first time, that the sediment characteristics (organic matter content and nutrient concentrations in interstitial water) under aquatic vegetation patches are dependent on patch length. To our knowledge, this is the first study investigating the effect of patch length on sediment and interstitial water characteristics in vegetated patches.

In the site LV, a clear minimal length threshold was observed at patch length $L = 0.9\text{m}$. Below this threshold patches had little effect on sediment characteristics, whereas, above this threshold, within-patch sediment had important effects on sediment characteristics, with 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 nitrogen forms in interstitial water were reversed compared to upstream position.

At the HV site, all patches (short and long) had higher concentrations, indicating either an absence of a minimal threshold length or a threshold length lower than the shortest patch studied (0.3 m). Contrary to our first hypothesis, in most cases, the sampling position did not have an effect on the sediment characteristics, probably meaning that the organic matter content and nutrient concentrations were similarly influenced from upstream to downstream, or in other words, that at the 10% position the effect of the patch was already substantial.

The organic matter content and nutrient concentrations in the interstitial water measured in the *C. platycarpa* patches were comparable to the values measured in sediment underlying dense patches of other submerged macrophytes species (Sand-Jensen 1998; Wigand *et al.* 2001; Schulz *et al.* 2003; Schneider and Melzer 2004; Cotton *et al.* 2006; Schoelynck *et al.* 2014). Indeed, in accordance with our third hypothesis, we demonstrated that the effect of patch length is dependent on site characteristics (i.e. trophic condition or sediment characteristics), with sites with different characteristics presenting different length thresholds.

The enrichment of sediment dissolved ammonia and phosphorus and depletion of nitrates indicate the establishment of anaerobic conditions in long patches at LV and in all the patches at the HV site. Indeed, the nutrient concentrations measured in long patches at LV and in all the patches at the HV site were similar or higher than the ones measured in the anaerobic zones of streams by Dahm *et al.* (1987). Sufficiently long and dense patches cause the reduction of flow velocity and the accumulation of fine sediment enriched in organic matter and nutrients (Dahm *et al.* 1987; Sand-Jensen 1998; Bruno and Kennedy 2000; Schulz *et al.* 2003). This leads to the establishment of anoxic conditions in the sediment by, first, the reduction of the surface-subsurface water exchange (Findlay 1995; Morrice *et al.* 1997), which limits the oxygenated water supplies, and, secondly, the increased consumption rate of the available oxygen that is requested by the decomposition processes (Sanders *et al.* 2007).

For long plant patches at both sites, the microbial respiration rate and the mean C:N of sediment were higher than the respective mean value measured in the upstream bare sediments, as stated in our first hypothesis. In short patches, the microbial respiration rate was low, probably due to the low quantity of organic matter available, even if the organic matter was fresh and highly labile (i.e. low C:N). In contrast, for long patches, the microbial respiration rate was high, likely due to the higher availability of organic matter. The high microbial activity was also confirmed by the low labile fraction (i.e. high C:N) which characterised the organic matter present in long patches. In long patches, the aerobic microbial decomposition of organic matter is probably limited to the interface with water, due

to the limited water exchange that permits sediment oxygenation (Findlay 1995; Morrice *et al.* 1997). The 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 in long patches.

As hypothesized, the presence of plant patches seems to have a significant effect on the relative importance of nitrification and denitrification processes, this effect probably mediated by the availability of oxygen in the within patch sediment. The steep increase of the ammonium proportion suggests that the anoxic conditions induce an inhibition of nitrification or that the ammonium uptake by the plants is too low to compensate the ammonium produced by ammonification (Ladd and Jackson 1982; Caffrey and Kemp 1992). At the same time, the decreased proportion of nitrates indicates an enhancement of the denitrification processes (Caffrey and Kemp 1992; Forshay and Dodson 2011). We can expect nitrate uptake by roots to be low because, first, ammonium uptake is usually preferred in aquatic plants (Nichols and Keeney 1976; Barko *et al.* 1991; Xie *et al.* 2005) and, secondly, the plants would probably present higher nitrate uptake from the water column due to the higher nitrate concentrations there. The absence of a patch threshold length at the site HV suggests that the effect on biogeochemical processes may be induced even for very short patches, due to the higher trophic conditions in this site or maybe a higher plant density.

In accordance with our first hypothesis, our results indicate an enhancement of denitrification, but not of nitrification in patches of *C. platycarpa*. In contrast, other previous studies demonstrated that aquatic patches enhance both processes of nitrification and denitrification relatively to bare sediment (Caffrey and Kemp 1992; Forshay and Dodson 2011). This difference in results may be due to the oxygen availability as a limiting factor for nitrification. Some species of macrophytes (both submerged and emergent) release oxygen by roots (Armstrong 1971; 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). *C. platycarpa* may not be able to efficiently release oxygen through its roots, which is confirmed by the presence of necrotic roots in plants of patches growing in highly organic sediment (pers. observations). The limited ability of *C. platycarpa* to release oxygen through roots may explain the absence of the enhancement of nitrification observed in other species. Therefore, the presence of different species with different physiologies (e.g. capacity to release oxygen by roots) will likely lead to different biogeochemical processes and therefore improve the heterogeneity of lotic ecosystems.

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

At the site LV, as hypothesized, plant height followed a quadratic pattern with the position downstream within the patch. Thus, up to a threshold length of 1.8m, patch height increased with length but decreased above this threshold suggesting a negative feedback effect. Contrary to our second hypothesis, the plant height at the upstream position was not linearly related to patch length but followed a quadratic pattern with identical threshold length of the downstream position.

At the site HV, plant height was not related to patch length, for both upstream and downstream positions. This could indicate that 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 plant response to hydrodynamic stress and sediment resources (Puijalon *et al.* 2008; Puijalon *et al.* 2011) but also the effects on biogeochemical cycles (Lavorel *et al.* 2007). Under a certain patch length, although plants are subject to hydrodynamic forces this has little or no effect on sedimentation (Bruno and Kennedy 2000), resulting in limited changes in interstitial water nutrient concentration with negative or no feedbacks for the plants. However, with increasing patch length, flow velocities and turbulence are reduced, reducing hydrodynamic stress for the plants (Bruno and Kennedy 2000). This promotes the accumulation of sediments and organic matter and nutrient concentrations increase, resulting in positive feedbacks favouring plant growth. Over a certain threshold length, plant growth reaches a maximal value and may then start to decrease indicating possible negative feedbacks. These negative feedbacks may be due to increased ammonium concentrations resulting from the cascading effect of the accumulation of organic matter (Fig. 5) which has been shown to have detrimental effects on plant growth (Britto and Kronzucker 2002; Jampeetong and Brix 2009). Toxicity seems to be species dependent with concentrations between 0.6 and 4.8mg l⁻¹ of ammonium reported to inhibit submerged plant growth or induce stress responses for the aquatic species *Potamogeton maackianus* A.Benn., *Vallisneria spiralis* (L.) L., *P. crispus* L. and *Groenlandia densa* (L.) Fourr., (Mattes and Kreeb 1974; Cao *et al.* 2004; Li *et al.* 2007; Cao *et al.* 2009). In our study, we measured less than 0.2mg l⁻¹ and between 1 and 10mg l⁻¹ of ammonium in interstitial water, respectively, for short and long patches in the LV site and between 0.4 and 1mg l⁻¹ whatever patch length for the HV site. The ammonium concentrations measured in long patches of *C. platycarpa* may explain the reduced plant height in the site HV and the presence of a threshold length in LV.

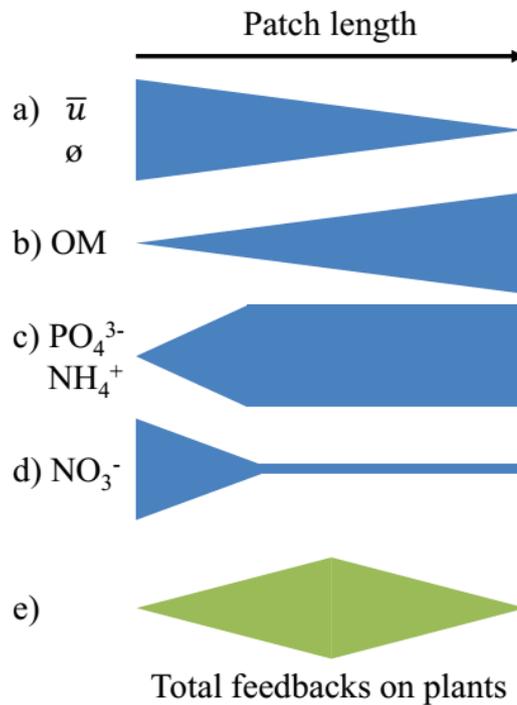


Fig. 5. Schematic model proposed for the effects of patch length on hydrodynamics and biogeochemical processes occurring inside the patch and the relative total feedbacks on plants in the streamwise dimension. (a) Main hydrodynamic factors interacting with plant patches (streamwise velocity, \bar{u}) and consequences for sediment deposition and resuspension (sediment texture, ϕ). Main chemical characteristics of the sediment: organic matter content (OM, b) of the sediment increases, concentrations of nutrients (orthophosphate, PO_4^{3-} , ammonium, NH_4^+ , and nitrate, NO_3^- , c-d) in interstitial water of sediment within a vegetation patch. Nutrient concentration and form depend on biogeochemical processes and plant uptake. (e) Feedback on plants resulting from the combined effect of the physical and biogeochemical processes.

4.4. Consequences for patch dynamics

Our results demonstrate that patch length has an important role in controlling the effects of patches on flow and sediment deposition, with cascading effects on biogeochemical processes and consequences for plant growth. Evidence points to the important role of these habitat modification processes and feedbacks with positive effects on plant growth up to a length threshold and then negative effects starting to limit further plant growth and patch expansion. These processes of habitat modification and following feedback may play an important role in plant patch dynamic with positive interactions in patches of short and intermediate lengths and negative ones in the long patches, possibly limiting patch expansion under certain conditions. The size distribution of natural patches is still unexplained. Previous studies reported a size distribution consisting of many patches of intermediate size (1-2 m long) and fewer patches of other sizes for *Callitriche* spp. and other aquatic species in lowland streams (Sand-Jensen and Madsen 1992; Sand-Jensen 1998; Sand-Jensen and Pedersen 1999; Schoelynck *et al.* 2012). Previous studies on the effect of patch length on the physical modification of flow and sediment demonstrated that a minimal patch length is required to observe a feedback for plants (Bruno and Kennedy 2000). Up to now, no maximal length thresholds over which negative feedbacks for plants may be induced have been observed if hydrodynamic stress is considered alone. However, this research suggests that when nutrient conditions are considered negative feedback, and hence a limiting condition to patch growth, may occur within long patches due to biogeochemical processes, particularly an accumulation of toxic concentrations of organic matter and ammonium. These maximal length thresholds will likely depend on environmental conditions, particularly trophic levels.

In particular, the threshold 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. Depending on plant and patch traits, it seems plausible that different aquatic plant species will have different effects on hydrodynamics and in turn the characteristics of accumulated sediments (Sand-Jensen 1998; Sand-Jensen and Pedersen 1999), which in turn have an effect on biogeochemical processes. Further investigations should therefore focus on the effect of patch length on the biogeochemical processes for plants with different morphological and architectural characteristics.

In conclusion, aquatic plant patches, and in particular the patches over a certain length, are biogeochemical hotspots (McClain *et al.* 2003), with higher rates of some microbial processes (e.g. denitrification), favouring the cycling of nutrients and organic matter.

Moreover, the regulation of biogeochemical processes by patch length may contribute to the patch dynamics ultimately limiting plant growth and patch expansion under certain conditions. The auto-regulation of patch lengths may maintain ecosystem patchiness and play key roles in ecosystem functioning. First, patchiness and the presence of patches of different lengths contribute to the heterogeneity of the ecosystem. The presence of , aerobic conditions in bare sediment and short patches and anaerobic zones in long patches, will influence nutrient conditions, with possible cascading consequences on the productivity and biodiversity of streams (Dahm *et al.* 1987). Secondly, regular pattern formation increases ecosystem resistance and resilience to disturbance (Rietkerk and van de Koppel 2008 and references therein): in the case of aquatic vegetation in lotic ecosystems, it has been hypothesized that patchiness increases plant resistance to mechanical damages induced by high discharge events, by diverting flows above and along the outer edges of patches (Schoelynck *et al.* 2012). Due to patch formation, the vegetation resisting high flow events may retain part of the fine sediment and the microbial community of the system, assuring the resilience of the stream ecosystems in term of biogeochemical processes.

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CHAPTER 3

Effect of Aquatic Plant Patches on Flow and Sediment Characteristics: The Case of *Callitriche platycarpa* and *Elodea nuttallii*

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Abstract In lotic ecosystems, submerged aquatic vegetation has important effects on hydrodynamic and sediment processes. These effects depend on plant morphology and patch structure. This study aimed to test the effect of 2 aquatic plant species on flow and sediment characteristics. For this purpose we measured under natural conditions 3D velocity profiles and sediment characteristics along the main axis of one patch of each species. The 2 species presented contrasting effects on velocity, turbulence profiles and sediment characteristics: one species had significant effects on hydrodynamics and accumulation of fine sediment also further downstream of the patch, whereas the second one accumulated very fine sediment mainly in the upstream half of the patch. These results emphasize the role of plant morphology on hydrodynamics and sediment physic-chemical characteristics.

1 Introduction

In freshwater lotic environments, interfaces between biota and sediment or flow are recognised as important regions where many critical biophysical processes occur, as recently reviewed by Marion et al. (2014). Particularly, complex and fundamental physical and biogeochemical processes occur at the plants-water-sediment interfaces (Carpenter and Lodge 1986). For instance, rooted submerged plants reduce velocity and increase sedimentation inside plant patches, and some species are able

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to oxygenate the substrate, influencing the microbial activity and hence the biogeochemical processes in the sediment. Submerged plants also induce important modification of flow conditions, acting as ecosystem engineers (*sensu* Jones et al. 1994) and increasing structural complexity and heterogeneity of lotic ecosystems. Plant patches behave as porous walls: on the one hand, they form an obstacle deviating the flow above and towards the sides of the canopy, locally increasing the velocity, whereas, on the other hand, the flow going through the patch shows a reduced velocity (Sand-Jensen and Mebus 1996; Sand-Jensen and Pedersen 2008, Vandenbruwaene et al. 2011). Consequently, the near-bed velocity, shear stress (James et al. 2004) as well as turbulence are significantly reduced inside the patches.

The changes in hydrodynamic conditions due to flow-plant interactions have indirect cascading effects on sediment dynamics: potential of resuspension and erosion are reduced, favouring sedimentation and reducing water turbidity (Hendriks et al. 2009; Sand-Jensen 1998; Schulz et al. 2003). Submerged plants also induce direct trapping of suspended particles and transported in bed-load through collisions with stem and leaf surfaces (Hendriks et al. 2008; Pluntke and Kozerski 2003). As a consequence, sediment accumulates inside the vegetation patches, with an increased proportion of fine particles compared to non-vegetated areas (Sand-Jensen 1998; Schoelynck et al. 2013).

The effect of aquatic plants on flow and sediment deposition depends on plant morphology and patch structure. For instance, species with dense canopies, as *Callitriche cophocarpa* Sendtn. and *Elodea canadensis* Michx., induce a high reduction of flow velocity inside their patches, increasing sediment retention (Sand-Jensen 1998; Sand-Jensen and Mebus 1996). On the contrary, species with open canopy, as *Sparganium emersum* Rehm., have less impact on flow and sediment dynamics (Sand-Jensen 1998; Sand-Jensen and Mebus 1996). Plant flexibility also influences the interactions: reconfiguration of flexible plants minimizes the surface area in contact with water, reducing the resistance to flow (Miler et al. 2012; O'Hare et al. 2007; Sand-Jensen 2003). At the plant level, the leaf area index (*i.e.* the ratio of leaf surface area to the ground area covered by the plant canopy) is an example of morphological traits that have been demonstrated to have a significant effect on the amount of fine sediment accumulated in submerged patches (Petticrew and Kalff 1992). However, only a few studies (Sand-Jensen 1998) have investigated simultaneously the effect of different plant morphologies on both flow and sediment characteristics (e.g. grain size, organic matter content, nutrient content ...). Sand-Jensen (1998) has analysed the effect of vegetation patches only on the streamwise component of velocity, although the flow can also be impacted on the lateral and vertical components.

The objective of the present study was to evaluate the effects of 2 submerged plant species having contrasting morphologies on different directional components of flow velocity and sediment characteristics. For this purpose, we carried out an in situ investigation of natural patches, combining 3D velocity, sediment grain size distribution and organic matter content measurements. An interdisciplinary

approach was applied for this study, as it is recognised fundamental to fully understand plants-water-sediment interactions (Marion et al. 2014). These complex interactions were then addressed and presented in an ecological perspective.

2 Materials and Methods

2.1 Study Sites and Plant Species

The study was conducted in two drainage channels of the Upper Rhône River (France), near the localities of Brégnier-Cordon (45° 38' 43"N, 5° 36' 29"E) and Peyrieu (45° 40' 46"N, 5° 42' 3"E). Drainage artificial channels were selected because they present uniform structure (cross-section, water depth) with long straight sections and natural colonization by submerged aquatic vegetation. The 2 channels presented similar length (2.1 and 2.8 km for Brégnier-Cordon and Peyrieu channels, respectively), width (6.0–8.0 m) and depth (0.6–0.7 m). These channels are fed by Rhône river seepage and hillslope aquifers. Cover by aquatic vegetation ranges from 30 to 90 % depending on season and channel section. The most abundant submerged species are *Callitriche platycarpa* Kütz., *Berula erecta* (Huds.) Coville, *Myriophyllum spicatum* L. and *Groenlandia densa* (L.) Fourr. in the site of Brégnier-Cordon, and *Veronica anagallis-aquatica* L. and *Elodea nuttallii* (Planch.) St.-John in the site of Peyrieu.

We selected two species with contrasting morphology and patch architectural structure: *Callitriche platycarpa* and *Elodea nuttallii*. *C. platycarpa* has thin, flexible and highly branched stems that can be 10–200 cm long (Tison and de Foucault 2014) and is heterophyllous: submerged leaves are opposite (*i.e.* two leaves per node), linear to narrowly oblanceolate and emergent ones are rhomboidal to obovate. At shoot apex, leaves get densely packed at the apex other forming a rosette. Plants of *C. platycarpa* tend to be organized in elliptic patches as flow pushes downstream the long stems generating an overhanging canopy. Patches are dense as stems get entangled, with most of the biomass concentrated in the upper part of the canopy. *E. nuttallii* has relatively rigid stems, 10–50 cm up to 150 cm long (Tison and de Foucault 2014), with few or no ramifications. Stems present three-leaved whorls densely packed and distributed almost uniformly along all their length. Patches of *E. nuttallii* are dense and compact with an elongated shape in direction of the flow and do not present an overhanging canopy.

2.2 Field Sampling

During summer 2014, one patch of *C. platycarpa* was sampled in Brégnier-Cordon and one patch of *E. nuttallii* in Peyrieu. These patches were selected because they

presented similar lengths (respectively 1.6 and 1.3 m) and were located as far as possible from the channel banks and from other patches to avoid hydrodynamical interferences.

For each patch, coupled measurements of hydrodynamics and sediment collection were carried out at five sampling points all along its central axis (2 outside and 3 inside plant patch). The 2 sampling points outside the patch were located approximately 1 m upstream from its leading edge (U) and 1 m downstream its rear edge (D). The 3 sampling points inside the patch were located at 10, 50, and 90 % of the canopy length. For each position, the velocity profile was measured and a core of sediment was collected (5 cm in diameter and 10 cm deep).

2.3 Velocity Profiles

Velocity vertical profiles were measured using a 3D Acoustic Doppler Velocimeter (ADV) (FlowTracker Handheld-ADV, SonTek). Vertical profiles consisted in depth steps of less than 12 cm, reduced to 1–4 cm near plants-water-sediment interfaces. For technical reasons, measurements closest to the sediment (near-bed) were taken at 4 cm above the channel bed. Velocity was recorded over 100 s at 1 Hz. For each component of velocity (streamwise, u ; spanwise, v ; vertical, w), mean velocity profiles (\bar{u} , \bar{v} , \bar{w}) were obtained and the turbulence intensity was quantified as the velocity variation around the mean (standard deviation). Standard deviation was then divided by the mean velocity to calculate the relative turbulence intensity.

2.4 Sediment Characterisation

The collected sediment cores were stored at 4 °C until measurements. To perform grain size analyses, sediments were wet sieved with distilled water at 1.6 mm and then dried at 70 °C for 48 h, to allow sample conservation until analyses were completed. Grain size analyses of sediment were carried out in aqueous phase by laser diffractometry, using a Malvern Mastersizer 2000 G (diameter range: 0.01–2000 μm). The analytical model used is based on the Fraunhofer theory and considers particles equal to spheres. Prior to the measurements, sediments were exposed to a treatment of ultrasound for 2 min to destroy the aggregated particles developed during the drying process, necessary for the preservation of the samples. The results of the analysis were displayed as grain size distributions curves. The mode of the curve indicates the most abundant grain size in volumic percentage present in the sample. The curves were then transformed in cumulative curves and the percentile values $d_{0.1}$, $d_{0.3}$, $d_{0.5}$ were calculated (maximum diameter corresponding to 10, 30 and 50 % of particle volume). The 3 values were correlated and only the percentile value $d_{0.3}$ was kept for analyses.

Finally, organic matter content was measured by weight loss after ignition at 550 °C for 2 h.

All the measurements were triplicated for each sample.

For each species, comparisons of sediment parameters relative to different positions were tested by one-way ANOVA, followed by a post hoc Tukey HSD correction. Linear regressions were performed to test the correlation between flow (near-bed velocities and relative turbulence intensities) and sediment parameters (grain size and organic matter content).

3 Results

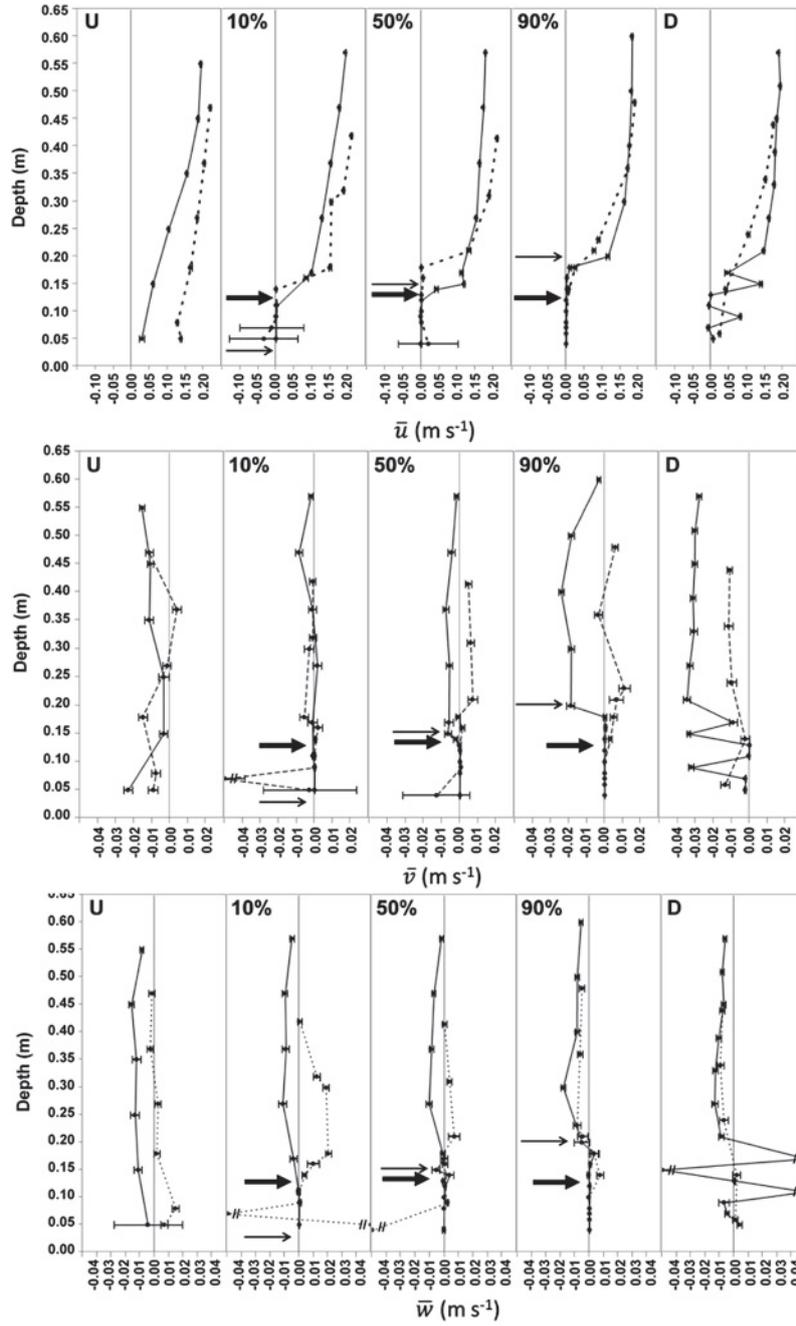
3.1 Velocity Profiles

Both species presented a different pattern of canopy height: the canopy height was relatively constant all over the patch length for *E. nuttallii*, whereas for *C. platycarpa* the canopy height gradually increased from the upstream to the downstream part of the patch (Fig. 1). For both species, velocity profiles upstream plant patch (U position) presented a steep decrease in streamwise velocity (\bar{u}) near the flow-sediment interface (Fig. 1). The profiles were more linear than logarithmic. For both species, the profiles downstream the patches (D position) were very similar to the upstream ones, except regarding the higher variability observed for *C. platycarpa*. For both species, \bar{u} decreased immediately above the canopy, reaching approximately 0 within the canopy.

Profiles of mean spanwise velocity (\bar{v}) showed little variation for *E. nuttallii*, with values ranging between 0 and 0.01 m s⁻¹. For *C. platycarpa*, \bar{v} increased above the canopy at the 50 and 90 % sampling points, due to flow deviation. At the D position, the velocity profile was more similar to the 90 % profile than to the U one but with a much higher variability.

For *E. nuttallii*, the \bar{w} slightly increased above the canopy at the 10 % position, due to upwelling, whereas at the 90 % position \bar{w} became negative, due to downwelling. For *C. platycarpa*, \bar{w} profiles were similar along its axis and presented mainly negative values, except a slight increase just above the canopy, at the 90 % position. At the D position, the velocity profile was very similar to the 90 % profile but with a higher variability.

For each direction and species, relative turbulence intensity increases at the flow-canopy and flow-sediment interfaces (Fig. 2). In the streamwise direction, relative turbulence intensity was higher for *E. nuttallii* than for *C. platycarpa*. The highest relative turbulence intensity was observed in the streamwise direction for *E. nuttallii*, and in the spanwise direction, above the canopy, for *C. platycarpa*.



◀ **Fig. 1** Mean vertical profiles of the three components of velocity (\bar{u} , \bar{v} , \bar{w}) for *E. nuttallii* (dashed line) and *C. platycarpa* (solid line), in the positions upstream (U), inside the patch at 10, 50 and 90 % of its length and downstream (D). The thick and thin arrows indicate the height of the patch for *E. nuttallii* and *C. platycarpa*, respectively

3.2 Sediment Characterisation

The grain size distribution curves were overall different for each species (Fig. 3). For *E. nuttallii*, two main modes were observed in each sampling position: a main mode around 350 μm and a secondary one around 60 μm . The sediment in the D position was the coarsest with a very homogeneous particle size around 450 μm . For *C. platycarpa*, the sediments texture was distributed around one main mode. The upstream sediment was the coarsest (main mode around 350 μm), whereas the sediment collected in the others positions were enriched in fine particles leading to an increase of particles with a silty texture (20–100 μm).

The two species presented different patterns of accumulation of fine sediment. For *E. nuttallii*, it decreased from the upstream position to a minimum at the 50 % position and then increased to a maximum reached at the D position (Fig. 4). For *C. platycarpa*, the $d_{0,3}$ was significantly higher at the U position than at all other positions.

No positive relationship was found between near-bed velocity (\bar{u} , \bar{v} , \bar{w}) and $d_{0,1}$ and $d_{0,3}$ for both species, whereas a positive linear relation was found between near-bed vertical relative turbulent intensity and $d_{0,3}$ (*E. nuttallii* $r^2 = 0.82$, $p < 0.05$; *C. platycarpa* $r^2 = 0.77$, $p = 0.05$).

The organic matter content ranged between 0.97 and 6.18 % of dry mass for *E. nuttallii*, and between 1.33 and 2.78 % for *C. platycarpa* (Fig. 5). For *E. nuttallii*, the organic matter content was maximal at the 50 % position and minimal at the D one. For *C. platycarpa*, the organic matter content was generally significantly higher within (10, 50 or 90 %) and downstream the patch. Organic matter tended to be inversely related to $d_{0,3}$ for both species (linear regression, $r^2 = 0.89$, $p = 0.01$, for *C. platycarpa* and $r^2 = 0.78$, $p = 0.06$, for *E. nuttallii*).

4 Discussion

In accordance with our expectations, the present results demonstrated that the two species had different effects on hydrodynamics, probably due to their differences in morphology and patch structure. *E. nuttallii* had a uniform canopy height and relatively rigid stems and deviated the flow towards the surface at the beginning of the patch, and then towards the streambed at the end of the patch. The upstream flow conditions were mainly restored downstream the patch. Relative turbulence intensity was higher inside the canopy and especially at the sediment-flow and canopy-flow interfaces. On the contrary, *C. platycarpa* had gradually increasing

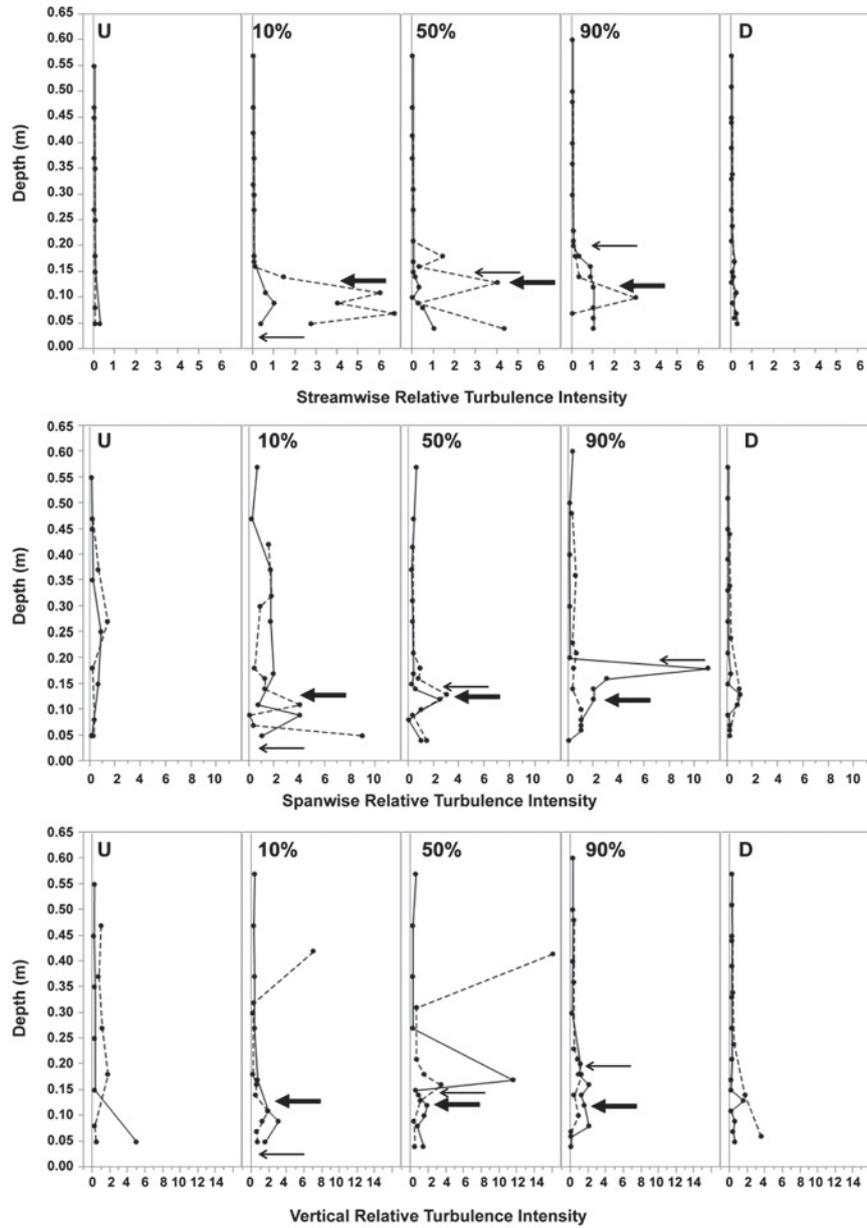


Fig. 2 Relative Turbulence Intensity of the three components of velocity (\bar{u} , \bar{v} , \bar{w}) for *E. nuttallii* (dashed line) and *C. platycarpa* (solid line). The *thick* and *thin* arrows indicate the height of the canopy for *E. nuttallii* and *C. platycarpa*, respectively. Positions are described in the legend of Fig. 1

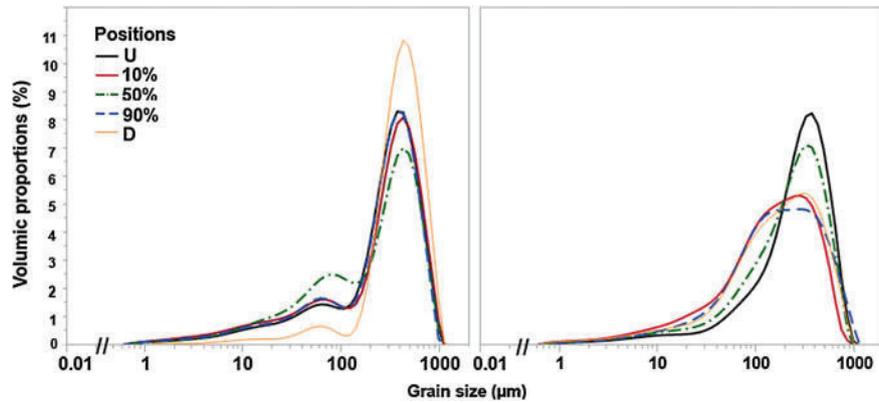


Fig. 3 Mean grain size distributions of sediment in different positions along the main axis of the patch of: (a) *E. nuttallii* and (b) *C. platycarpa*. Positions are explained in the legend of Fig. 1

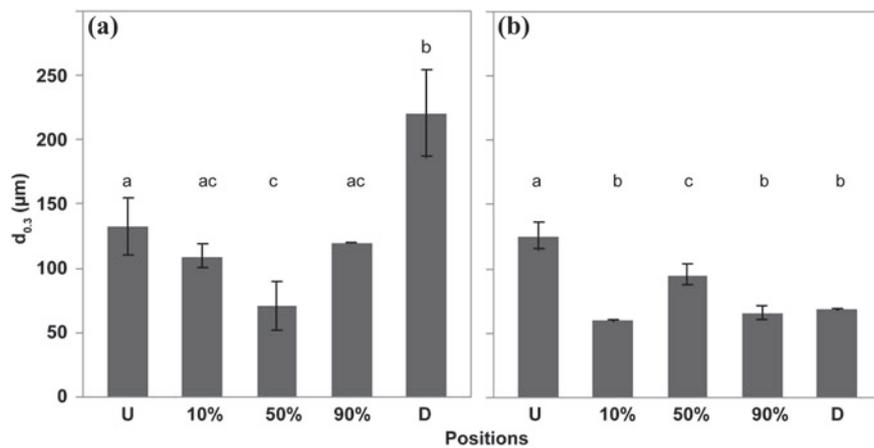


Fig. 4 Mean value of $d_{0.3}$ in sediment collected in different positions along the main axis of the patches of: (a) *Elodea nuttallii* and (b) *Callitriche platycarpa*. The positions are described in the legend of Fig. 1. Bars with different letters are significantly different (one way ANOVA, followed by post hoc Tukey's HSD correction, $p < 0.05$)

biomass and canopy height from upstream to downstream. When the flow encountered the dense canopy, the flow was deviated on patch side, creating high spanwise relative turbulence at the canopy-flow interface. The effects of the patch of this species on hydrodynamics were also observed further downstream the patch. Similar effects of *C. platycarpa* on hydrodynamics were previously reported in literature (Schoelynck et al. 2012, 2013).

As expected, both species also induced contrasting effects on sediment characteristics. The effects observed for the patch of *C. platycarpa* were consistent with its

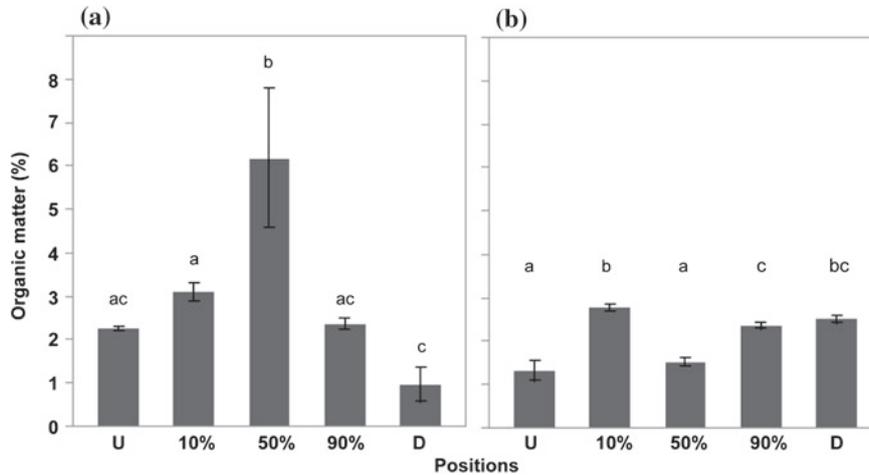


Fig. 5 Mean value of organic matter content (%) in sediment collected in different positions along the main axis of the patches of: (a) *Elodea nuttallii* and (b) *Callitriche platycarpa*. The positions are described in the legend of Fig. 1. Bars with different letters are significantly different (one way ANOVA, followed by post hoc Tukey's HSD correction, $p < 0.05$)

effect on hydrodynamics: $d_{0.3}$ revealed that very fine sand and coarse silt were trapped not only within the patch, but deposited also downstream the patch, consistently with previous results (Schoelynck et al. 2013). On the contrary, the patch of *E. nuttallii* trapped most of the sediment in the upstream half of the patch and the finest sediment in the middle part of the patch. No fine sediment was accumulated in the downstream half of the patch, possibly because the trapping was high enough to deplete the suspended sediment that moved inside the patch. Similar patterns were observed for species *E. canadensis*, morphologically similar to *E. nuttallii* (Sand-Jensen 1998).

The two species influenced also the accumulation of organic matter inside and downstream the patch, showing contrasting patterns. The negative relation observed between the $d_{0.3}$ and the organic matter seemed to indicate that the finer sediments were enriched in organic matter. Moreover, the two species showed a significant difference in the amount of organic matter percentage accumulated within and downstream the patch. *E. nuttallii* and *C. platycarpa* thus had contrasted action on organic matter content in sediment. High concentration of organic matter in anaerobic conditions can lead to the accumulation of soluble organic compounds and other substances that are potentially toxic for plants (Barko and Smart 1983). Therefore, differences in organic matter could have consequences for the growth of both species, especially in the downstream part of the patch, where patch usually tends to develop. For *E. nuttallii*, the sediment downstream patches had a low organic matter content, possibly without limitation for plant growth. For *C. platycarpa*, instead, the sediment downstream the patch presented a similar value than within the patch and higher than upstream, potentially limiting plants growth.

Contrary to previous studies, no positive relationship was found between near-bed velocity and $d_{0.1}$ and $d_{0.3}$ for both species (Sand-Jensen 1998). This lack of correlation could be due to the too low number of sampling points in our study. However a positive correlation was found between near-bed vertical relative turbulent intensity and $d_{0.3}$, underlining the importance of the vertical component of turbulence in the processes of deposition (and resuspension) of fine sediment particles.

Our results emphasize the role of morphological and structural factors in the effects of submerged vegetation on flow and sediment processes. For instance *E. nuttallii* has relatively rigid stems and almost a uniform height all over the patch length. On the contrary *C. platycarpa* has flexible stems and most of the biomass located in the upper part of the canopy: the upstream part of the canopy, with less biomass, is more subject to flow pressure and is then compressed near the sediment bed, whereas further downstream plants gradually increment their biomass acquiring buoyancy and then increasing the patch height. This morphological and structural difference influences the relative depth of submergence (H/h , flow depth to canopy height ratio; Nepf 2012). The patch of *E. nuttallii*, with a uniform height, had a constant relative depth of submergence, corresponding to shallow submerged ($H/h < 5$). On the contrary, the patch of *C. platycarpa* presented a varying relative depth of submergence along the length ranging from deeply submerged ($H/h > 10$) to shallow submerged ($H/h < 5$) or even to emergent ($H/h = 1$) when the patches reach the surface. As differences in relative depth of submergence correspond to different flow and turbulence structures (Nepf 2012), they could explain the contrasting effects on both hydrodynamics and sediment composition (*i.e.* mass transport) for the two species. As other morphological and structural properties of vegetation have an effect on hydrodynamics and sediment composition (*e.g.* stem/leaf length, leaf surface, flexibility, patch size ...), further in situ studies with combined measurements of several morphologies, hydrodynamics and sediment composition are necessary to understand the relative effect of these characteristics on flow and sediment dynamics.

This study showed how morphology and patch structure substantially controlled the effects of vegetation on flow and sediment dynamics, not only inside the patch but also downstream the patch. The presence of different species in lotic ecosystems as streams may contribute to the hydrodynamical and geomorphological heterogeneity of these systems.

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DISCUSSION

The objective of my thesis was to study the role of plant and patch architectural characteristics in the processes that trigger positive and/or negative feedbacks for plants and how the environmental conditions affect these processes. A multidisciplinary approach improved the understanding of submerged aquatic patch interactions with the environment and their consequences for patch dynamics in lotic ecosystems, including the feedbacks for plants. Previous studies investigated principally the effect of patches on hydrodynamics and on sediment characteristics (e.g. texture, Sand-Jensen and Mebus 1996; Sand-Jensen 1998; Sand-Jensen and Pedersen 1999; Schoelynck *et al.* 2012; Schoelynck *et al.* 2013; Schoelynck *et al.* 2014) or on nutrient concentrations and biogeochemical processes alone (Schulz *et al.* 2003; Schneider and Melzer 2004; Schulz and Kohler 2006). My thesis integrated the effects of aquatic plants on hydrodynamics, sediment characteristics, biogeochemical processes and the plant responses (Fig. 6). In particular, the role of patch size in these interactions was studied, in order to investigate the mechanisms that influence patch growth in the longitudinal dimension. Both a minimal and maximal threshold of patch length necessary to induce respectively positive and negative feedbacks were found. Moreover the studies were effectuated on sites with different environmental conditions, which enable to address the question of the importance of habitat conditions in these processes. Finally, the role of traits and patch architectural characteristics were explored.

1. Effects of patch length on hydrodynamics, sediment, biogeochemical processes

Effects of patch length on hydrodynamics and sediment characteristics

My studies confirmed that aquatic plant patches in lotic systems have an effect on the physical habitat, in particular hydrodynamics and sediment texture, and, for the first time, demonstrated how this effect depends on patch size. The velocity linearly decreased with increasing patch length, although in-patch velocities were only available for the longest patches ($L > 1.1$ m), and this conclusion is limited to a depth of 20 cm. These results were consistent with previous studies (Schoelynck *et al.* 2013; Schoelynck *et al.* 2014). The reduction of sediment texture within the patch was also related to patch size: $\Delta d_{0.3}$ exponentially decreased with patch length. Moreover, these results indicated that the physical modification of the habitat presented a minimal patch size threshold necessary for the modification to occur and have a positive influence on plants. Flow velocity at 20 cm of water depth was reduced only for patches with $L > 0.65$ m, while sediment texture was reduced

starting from patches with $L > 0.3$ m and texture became finer up to a patch length over which no modification of sediment texture was observed (Tables 2, 3).

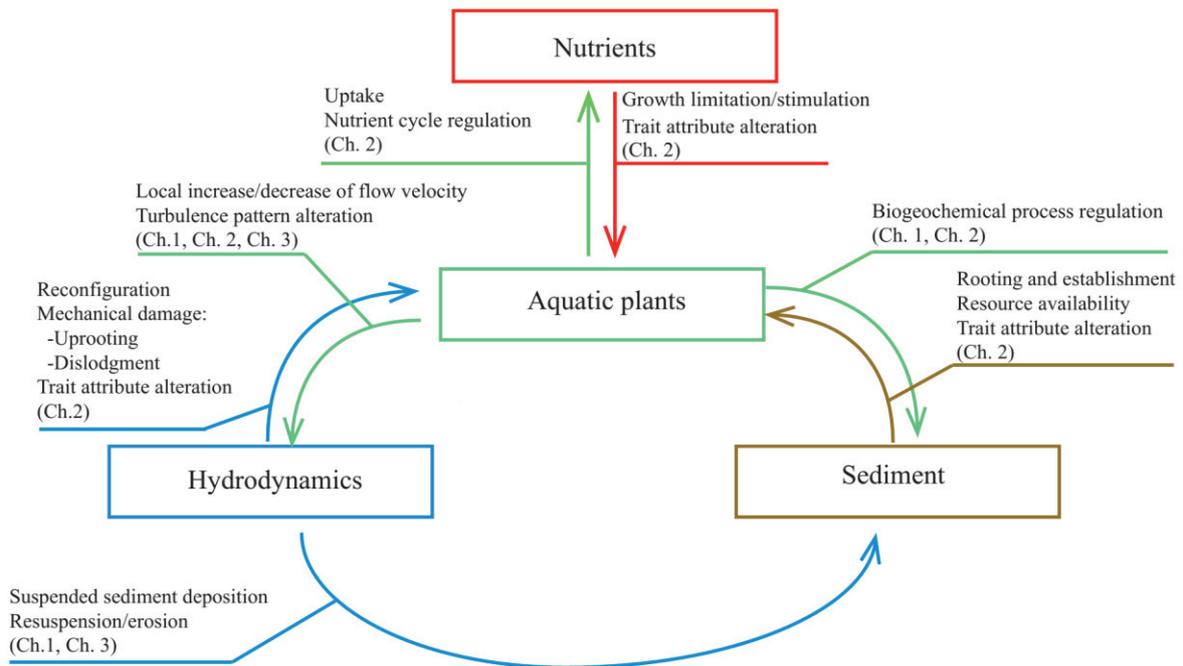


Fig. 6. Conceptual model representing the feedback loop for the aquatic vegetation and its abiotic components of lotic systems. The interactions discussed in the chapters of my thesis are indicated. Submerged aquatic plants influence and are influenced by the hydrodynamics, the sediment characteristics and the nutrients characteristics. The different colours correspond to the different components of the feedback loop and their actions on other components (green for submerged aquatic plants, blue for the hydrodynamics, brown for sediment and red for nutrients).

SITE	L (m)	\bar{u}_{20} (m s ⁻¹)	$\Delta\bar{u}_{20}$ (%)	$d_{0.3}$ (μ m)	$\Delta d_{0.3}$ (%)	OM (%)	Δ OM (%)	PO ₄ ³⁻ (ppm)	Δ PO ₄ ³⁻ (%)	NH ₄ ⁺ (ppb)	Δ NH ₄ ⁺ (%)	NO ₃ ⁻ (ppm)	Δ NO ₃ ⁻ (%)
LV	0.16	0.17	1.44	60.26	0.00	1.65	9.30	61.17	-14.7	40.52	-19.3	2.41	12.8
	0.33	0.16	0.30	52.48	-33.9	2.66	18.9	91.35	26.7	52.13	133	3.47	-22.8
	0.90	0.14	22.0	19.95	-66.9	10.1	300	2802	1568	5146	879	0.60	-81.5
	1.60	0.11	35.7	95.71	-24.1	1.53	14.9	1995	-46.3	4084	94.8	0.33	47.1
	2.27	<0.01	-110	39.81	-49.9	4.33	285	383.2	362	3037	827	0.52	-85.0
HV	3.13	<0.01	-100	52.48	-12.9	3.44	17.3	1010	1243	2538	1697	0.52	-27.3
	0.30	0.25	5.79	144.9	44.6	0.90	0.72	140.5	113	887.8	16.5	0.49	-80.1
	0.65	0.14	-18.6	79.43	-42.5	1.64	137	348.9	444	442.5	131	0.04	-84.4
	0.85	0.07	-69.2	19.95	-85.6	7.95	635	187.0	106	502.6	182	0.42	-77.8
	1.45	0.10	-922	18.24	-80.0	7.16	464	593.9	378	363.0	54.7	12.9	-3.12
1.90	<0.01	-99.4	22.91	-78.1	7.88	857	299.2	863	470.9	456	0.41	191	
2.50	0.08	-61.0	41.78	-74.9	3.11	270	199.6	38.0	747.8	44.5	6.59	640	

Table 2. Synthesis of the parameters measured in the middle of *Callitriche platycarpa* patches of increasing length (L) in two drainage channels of the Rhône river in the chapters 1 and 2: time-averaged streamwise velocity at 20 cm (\bar{u}_{20}), sediment texture ($d_{0.3}$), sediment organic matter content (OM) and nutrient concentrations in interstitial water (PO₄³⁻, NH₄⁺, NO₃⁻). Each parameter has been reported as its absolute value and as its relative value to a reference upstream position (1 m upstream of the patch upstream edge). The symbol Δ indicates the relative value. A positive relative value indicates an augmentation of the parameter value compared to the upstream condition, while a negative relative value indicates its reduction.

Parameter	Site	Min. patch size threshold (m)	Max. patch size threshold (m)
\bar{u}_{20}	LV	>0.65 (-)	
	HV	>0.65 (-)	
$d_{0.3}$	LV	>0.3 (-)	0.33 (=)
	HV	>0.3 (-)	1 (=)
OM	LV	≥ 0.9 (+)	
	HV	≥ 0.65 (+)	
NH_4^+ , PO_4^{3-}	LV	>0.9 (+)	
	HV	≥ 0.3 (+)	
NO_3^-	LV	>0.9 (-)	
	HV	≥ 0.3 (-)	

Table 3. Minimal and maximal patch size thresholds found in the chapters 1 and 2 to induce a modification of hydrodynamics (\bar{u}_{20}), sediment characteristics ($d_{0.3}$, OM) and nutrient concentrations (NH_4^+ , PO_4^{3-} , NO_3^-). The sign in parenthesis indicates if the parameter value increases (+), decreases (-) or remains unchanged (=) over the patch size threshold.

Effects of patch length on biogeochemical processes through its effects on hydrodynamics and sediment characteristics

The reduction of flow velocity and consequent accumulation of fine sediment should lead to a reduced porosity and water exchange between sediment and surface water, which should lead to reduced oxic condition, with cascading consequences for the biogeochemical processes (Hargrave 1972; Findlay 1995; Morrice *et al.* 1997; Gutiérrez and Jones 2006). As the plant-induced modifications to flow velocity and sediment characteristics depended on patch size, the hypothesis was that the effect of aquatic plant patches on the biogeochemical processes also depended on the patch size. In the site LV, a clear threshold at $L=0.9$ m was necessary for the patches to have a strong effect on the organic matter content in sediment and nutrient concentration (Tables 2, 3). In particular, the within-patch sediment of long patches showed increased organic matter content, orthophosphate and ammonium concentrations and decreased nitrate concentration in interstitial water compared to the upstream position (Table 2). Interstitial water nutrient concentrations resulted from the effects of the plant-induced modification of the physical conditions on the biogeochemical processes and plant root uptake (Chambers *et al.* 1989; Gutiérrez and Jones 2006). My results indicated an increased microbial respiration rate and suggested a reduction of nitrification rate and an increased denitrification rate within long patches of *C. platycarpa*. As a result, the relative

concentrations of ammonium and nitrates in interstitial water were reversed in short patches compared to long ones. Similar results were found by Marmonier et al. (unpublished data) in other vegetate patches dominated by *Callitriche* spp. in the Tamoute River in the northern part of Brittany. In this site, the ammonium concentrations in interstitial water within the patches were high ($2.17 \pm 0.26 \text{ mg l}^{-1}$) and higher compared to bare sediment ($0.49 \pm 0.37 \text{ mg l}^{-1}$). In the Tamoute River, the accumulation of ammonium within the patches was probably due to low oxygen concentrations available for ammonium oxidation (below 2 mg l^{-1}). Indeed, low oxygen concentrations limit the nitrification activity in the field, as proven by the ammonium accumulation. The limiting oxygen conditions for within-patch sediments in the field were confirmed by the high potential nitrification rates measured in the laboratory in oxic conditions ($287 \pm 123 \text{ ng}_N \text{ g}^{-1} \text{ h}^{-1}$). Contemporarily, the nitrate concentrations were very low within the patches ($2.16 \pm 2.81 \text{ mg l}^{-1}$) and lower compared to bare sediments ($5.19 \pm 6.23 \text{ mg l}^{-1}$). The loss of nitrate within vegetated sediment was probably due to the denitrification process occurring at low oxygen concentrations. Indeed, in the laboratory were measured high rates of potential denitrification in anoxic conditions (with the addition of both glucose and nitrate, $289 \pm 145 \text{ ng}_N \text{ g}^{-1} \text{ h}^{-1}$).

2. Role of environmental conditions on the effect of patch length on hydrodynamics, sediment and biogeochemical processes

The effects of patch length on flow reduction did not differ between sites with slightly different flow conditions, indicating that patch length had similar effects on flow reduction even under relatively different environmental conditions. Likewise, previous studies showed very similar flow velocities in patches of the same species in different streams (Sand-Jensen and Pedersen 1999). Indeed, the capacity of modifying the surrounding physical environment is a species-specific property that depends on plant morphological traits and canopy architecture (Fonseca and Fisher 1986; Sand-Jensen 1998; Sand-Jensen and Pedersen 1999; Bouma *et al.* 2010; Schoelynck *et al.* 2014).

In contrast, different effects of patch length were observed on sediment texture between sites. In particular, the sites investigated presented two different maximal patch length thresholds over which the minimal sediment texture was reached and did not change with increasing patch length. The values of minimal sediment texture were also different for the two sites. The different relationship between patch length and sediment texture in the two sites could be caused by a difference in suspended sediment available at the sites: sites with

lower values of sediment texture (HV) may have finer sediment in suspension, which requires lower velocities to deposit all ranges of suspended particle sizes, including the finest ones. As very low flow velocities are found only in long patches, the finest sediments are present only in the long patches (for HV, $L > 1.0$ m). Reciprocally, sites with a coarser sediment texture (LV) may have suspended particles of larger dimension; in this case, even the finest range of particles available would tend to deposit at higher near-bed velocities and therefore even in smaller patches (for LV, $L > 0.33$ m). The differences observed between the two sites may also be due to differences in plant morphology (*e.g.* stem density), leading to reach a minimum flow velocity within the patch at different lengths, resulting in different sediment deposition patterns (Chen *et al.* 2013).

The effects of patch length on the within-patch accumulation of organic matter did not differ between sites. However, the organic matter accumulated within long patches (2.3-2.5 m) in the site HV was more refractory compared to the site LV, where organic matter was more labile (Ittekkot 1988).

The site HV presented higher trophic conditions compared to the site LV. Increasing the trophic level, the effect of patches on the biogeochemical processes occurred for shorter patch length compared to the site with a lower trophic level (LV). The higher nitrate concentrations in surface waters have been demonstrated to increase the denitrification process rate (García-Ruiz *et al.* 1998; Royer *et al.* 2004; Silvennoinen *et al.* 2008). In the site HV, the reduction of nitrates within the patches started already for small patches ($L = 0.3$ m), while in the site LV the nitrate reduction started for patches with $L \geq 0.9$ m. Similarly, the accumulation of orthophosphate and ammonium was already at saturation in the site HV, while a strong accumulation of these nutrients was observed only for patches with $L \geq 0.9$ m in the site LV.

3. Effects of patch length on the feedbacks for plants

In the site LV, plants of patches of increasing size showed a maximal growth at $L = 1.8$ m. The increase of plant growth up to $L = 1.8$ m indicates the presence of positive feedbacks for plants up to this threshold length. Possible positive feedbacks could be related to flow reduction within patches. Flow velocity was related to patch length by an inverse linear relation (Chapter 1), indicating that plants in longer patches are subject to lower mechanical stress. For $L \geq 0.9$ m a strong increase of nutrients in interstitial water was observed (Chapter 2), reducing possible nutrient limitations for plant uptake by roots. Both flow velocity

reduction and increased nutrient availability should be beneficial for plants and explain the increase of plant height for patches up to $L=1.8$ m. Oppositely, the reduction of patch height over this threshold seems to indicate that, for longer patches negative feedbacks for plants occur. These negative feedbacks cannot be due to the reduction of flow velocity, as the velocity reduction should not limit plant photosynthesis. Indeed, even in long patches (up to 5m) the flow velocity is usually high enough for providing the carbon dioxide necessary for photosynthesis (Sand-Jensen and Mebus 1996). One possible negative effect could be due to the high contents of refractory organic matter in sediment or other phytotoxins such as ammonium which, despite being a nutrient for plants, can be toxic at high concentration (Barko and Smart 1983; Britto and Kronzucker 2002; Nimptsch and Pflugmacher 2007). Ammonium toxicity for aquatic plants has been investigated and quantified for several aquatic species (Cao *et al.* 2004; Nimptsch and Pflugmacher 2007; Cao *et al.* 2009; Yu *et al.* 2015) but not for *C. platycarpa*. For the aquatic species *Potamogeton maackianus* A.Benn., *Vallisneria natans* (Lour.) H. Hara, *P. crispus* L. and *Groenlandia densa* (L.) Fourr., ammonium concentrations between 0.6 and 4.8mg l⁻¹ inhibit plant growth or induce stress responses. (Mattes and Kreeb 1974; Cao *et al.* 2004; Li *et al.* 2007; Cao *et al.* 2009). In our study, we measured less than 0.2mg l⁻¹ and between 1 and 10mg l⁻¹ of ammonium in interstitial water respectively for short and long patches in the LV site. The ammonium concentration measured in long patches of *C. platycarpa* in LV may limit plant growth, which could explain the presence of a threshold length, over which plant height decreases for increasing patch length.

In the other site studied, HV, the effect of plant patches on biogeochemical processes was observed for all the patch sizes, without threshold length. In this site, plant height was not related to patch length. However, a slight increase of patch height was observed for small patches. This increase should be due to the reduction of hydrodynamic stress that occurs on a short length from the patch leading edge. The ammonium concentrations measured in long patches of *C. platycarpa* were between 0.4 and 1 mg l⁻¹ whatever the patch length for the HV site. In addition, the ammonium was the prevailing nitrogen form for at least one sampling position within the patch, whatever the patch length. Indeed, the environmental conditions in this site, in particular the higher trophic level may affect plant growth, resulting in a lower plant height compared to the measured ones in LV, a site presenting a lower trophic level. Indeed, it has been demonstrated that nitrogen concentration (NH₄⁺ and NO₃⁻ combined together) reduces plant growth over 4 mg l⁻¹ and is even lethal over 10 mg l⁻¹ for submerged

plants as *Elodea* spp. (Ozimek 1993). In addition, the longest patches observed in the field were shorter than in the LV site (personal observation), indicating that a negative feedback along the patch occurred for a shorter patch length.

4. Role of plant traits and patch architectural characteristics in plant-flow-sediment interactions and feedbacks for plants

The physical habitat modification depends on plant morphology and patch structural architecture (Sand-Jensen 1998). In Chapter 3, I confirmed that a submerged aquatic species, as *Elodea nuttallii*, with relatively rigid stems, relatively sparse and with a uniform patch canopy height has different effects on hydrodynamics and sediment characteristics compared to a more flexible and dense species with an overhanging canopy such as *C. platycarpa*. The first type of plant morphology and patch architecture (*E. nuttallii*) deviated the flow principally above the canopy and generated turbulence related to stems at the upstream edge of the patch with consequent accumulation of fine sediment and organic matter principally in the middle of the patch. The second type of plant morphology and patch architecture (*C. platycarpa*) deviated the flow principally next to the patch, influencing flow and sediment characteristics both within the patch and downstream the patch with a resulting accumulation of fine sediment with high organic matter content not only inside the patch but also downstream the patch. These results were consistent with previous studies on the same species (*C. platycarpa*) and species with similar morphologies (*Callitriche cophocarpa* Sendtn. and *Elodea canadensis* Michx., Sand-Jensen and Mebus 1996; Sand-Jensen 1998; Schoelynck *et al.* 2012; Schoelynck *et al.* 2013)

Plants with different morphological traits and patch architectural characteristics should have different effects on the plants-flow-sediment interactions, with different consequences not only for the physical habitat, but also for the biogeochemical processes and the relative feedbacks for plants. The patch size threshold over which positive or negative feedbacks occur should then vary not only depending on site characteristics, but also on the morphology of the species forming the patches. I expect that patches of species with morphologies similar to *Elodea nuttallii*, with relatively open canopies and low canopy height would have reduced effects on the feedback loop, in particular resulting in a limited accumulation of organic matter and phytotoxins within patches. As a consequence, I expect the absence of negative feedback induced by the biogeochemical processes whatever the patch length for species

comparable to *Elodea nuttallii*. For species with higher patch density and canopy height, a patch size threshold over which negative feedbacks for plant occur would probably appear, induced by the biogeochemical processes. This threshold should occur for shorter length for species with denser and higher canopy, as these architectural characteristics increase the patch capacity to trap fine sediment and organic matter (Bouma *et al.* 2007; Bouma *et al.* 2009; Nepf 2012). The patch size threshold should be also dependent on the physiology of aquatic plants, as plant able to release oxygen by roots would probably reduce the negative feedbacks due to the accumulation of organic matter (Barko and Smart 1983; Sand-Jensen *et al.* 2005; Lemoine *et al.* 2012; Racchetti *et al.* 2017).

In summer 2015, during a preliminary study, I investigated the role of plant and patch characteristics on the feedbacks for plants, comparing three species with contrasting morphologies and patch architecture. Figure 7 presents preliminary results consisting of the height of plants collected in summer 2015 belonging to patches of increasing length for three species with different morphologies and patch architectural characteristics: *Groenlandia densa* (L.) Fourr., *Berula erecta* (Huds.) Coville and *C. platycarpa*. *G. densa*, which has morphology and patch architecture comparable to *E. nuttallii*, does not present a relation between plant height and patch length (linear model, $R^2=0.02$, $p=0.80$). We can suppose that there are no negative feedbacks for this species in the site where plants were collected (HV). Instead, for *B. erecta*, which presents a rosette of petiolated dissected leaves, with intermediate density between *G. densa* and *C. platycarpa*, a significant polynomial relation between plant height and patch length was observed ($H=-6.9L^2+35L+10$; $p<0.05$), indicating that negative feedbacks occur for *B. erecta* over a threshold length of 2.55m. This threshold is longer to the one observed for *C. platycarpa* ($L=2$ m; $H=-24 L^2+96L-21$; $p=0.18$).

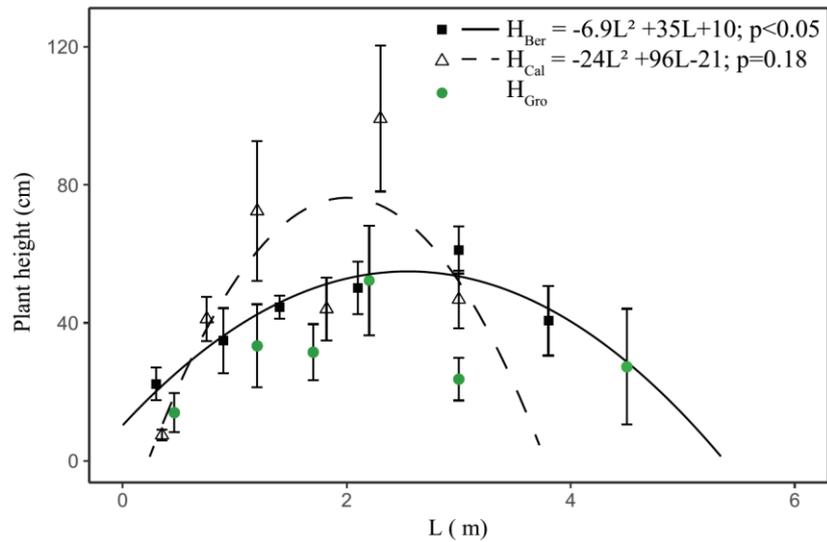


Fig. 7. Effect of patch length (L) on plant height (H), a proxy for plant growth, along patches of *Groenlandia densa* (green dots), *Berula erecta* (black squares and solid line) and *C. platycarpa* (white triangles and dashed line). The points and error bars represent the mean and standard deviation, respectively, of plant height for specimens (n=5) collected in patches of increasing length. All plants were harvested in the site HV at 90% of the patch length.

5. Consequences of the patch size effects on flow, sediment and biogeochemical processes for patch dynamics

As physical ecosystem engineer, submerged aquatic plants induce important habitat modifications with consequent feedbacks for plants that may drive plant patch dynamics (Carpenter and Lodge 1986). In particular the patch effects on flow and sedimentation patterns and their consequences on the biogeochemical processes depend on patch length. The plant-induced habitat modification has feedbacks for plants, influencing plant growth, which depends on patch length.

In literature, authors observed that patchy submerged aquatic vegetation in lotic systems is often constituted by many patches of intermediate size (1-2 m long) and fewer patches of other sizes (Sand-Jensen and Madsen 1992; Sand-Jensen 1998; Schoelynck *et al.* 2012). My results could explain this size distribution of natural patches. I demonstrated that, in lotic ecosystems, a minimal size threshold is necessary for positive feedbacks on submerged species to occur. A minimal size threshold necessary to induce positive feedbacks for plants was previously demonstrated for salt marsh patches, which are exposed to mechanical stress generated by tides and waves (Bruno and Kennedy 2000; Bos *et al.* 2007). In addition, I demonstrated that over a certain patch length negative feedbacks for plants occur, limiting

patch growth whereas up to now, no such maximal size thresholds had been observed if hydrodynamic stress was considered alone. Therefore, through the effect that patches have on the modification of the flow velocities and on sedimentation patterns and therefore on sediment characteristics and biogeochemical processes, aquatic patches self-regulate patch size, leading to a spatial self-organisation (Rietkerk and van de Koppel 2008; Schoelynck *et al.* 2012; Cornacchia *et al.* 2018).

The maximal size thresholds may depend on environmental conditions that are fundamental drivers of patch dynamics. In particular, flow velocities control the patch expansion especially on alongside dimension (Schoelynck *et al.* 2012). On a longitudinal dimension, the patch expansion may be instead regulated directly by biogeochemical processes that would themselves likely depend on sediment characteristics (as organic matter and nutrient contents) within the patch and on hydrodynamic conditions, which influence the sediment characteristics. As high quantities of organic matter may induce the accumulation of phytotoxins (Barko and Smart 1986 and references therein), the quantity and quality of particulate organic matter in the system available for trapping may also represent important factors to consider. The trophic level of the lotic system may also play an important role for patch dynamics, directly influencing the biogeochemical processes (García-Ruiz *et al.* 1998; Silvennoinen *et al.* 2008), but most importantly impacting plant and patch development through increased effects of the patches on the biogeochemical processes (thresholds over which negative feedbacks are triggered occurring for shorter patch lengths) and by increasing the magnitude of the effect on plants (*i.e.* reduced plant height).

Different effects on submerged vegetation should occur for different flow and trophic conditions. Low velocities should favour lateral patch expansion up to reach a full vegetation cover of the stream bed width, as no negative feedbacks induced by flow would occur on a alongside dimension, due to the attenuation or nullification of the mechanical stress. On a longitudinal dimension, the reduction of flow velocity will still enhance fine sediment trapping within the vegetation, with a consequent increase of the nutrient availability and organic matter, stimulating plant growth. At low trophic levels, the ammonium concentration and organic matter may be sufficiently low not to trigger negative feedbacks along the patches, which may therefore expand with no limitation on a longitudinal dimension too. Therefore, a full cover of submerged aquatic plants would be expected at low velocities and low nutrient concentrations (Fig. 8). In systems with low velocities and high trophic level, submerged aquatic vegetation would be most likely over-competed by planktonic, benthonic

algae and aquatic plants more typical of lentic and eutrophic waters (Hilton *et al.* 2006) (Fig. 8). Intermediate velocities would instead favour the formation and maintenance of submerged vegetation patchiness on an alongside dimension due to the negative feedbacks induced by the flow acceleration and reduced sedimentation next to the patch (Schoelynck *et al.* 2012). On a longitudinal dimension, the patch expansion should be regulated directly by biogeochemical processes. In this case, low trophic conditions may induce reduced control on the patch expansion that should mainly be regulated by the hydrodynamic characteristics, resulting in long streamlined patches. For increasing trophic level, patches may have a more important effect on biogeochemical processes in a shorter length, so that negative feedbacks for plants would occur for shorter patches compared to lower trophic level conditions, inducing the limitation of plant growth and patch expansion. The limitation of plant growth and patch expansion should then facilitate the succession to a system dominated by other aquatic plants more typical of eutrophic waters or even algae (Fig. 8). Finally, very high velocities would impede the development of vegetation (Puijalon and Bornette 2013 and reference therein) independently of the trophic level (Fig. 8).

Moreover, the trophic level has a direct effect on the plant traits. The increase of nutrient concentrations has been demonstrated to weaken the plant tissues (Lamberti-Raverot and Puijalon 2012), resulting in a reduction of mechanical resistance for plants, and therefore increasing plant vulnerability to hydrodynamic stress. In conclusion, to understand the patch dynamics in a particular lotic system it is important to take in consideration the specific environmental conditions, integrating hydrodynamics, sediment characteristics and trophic level.

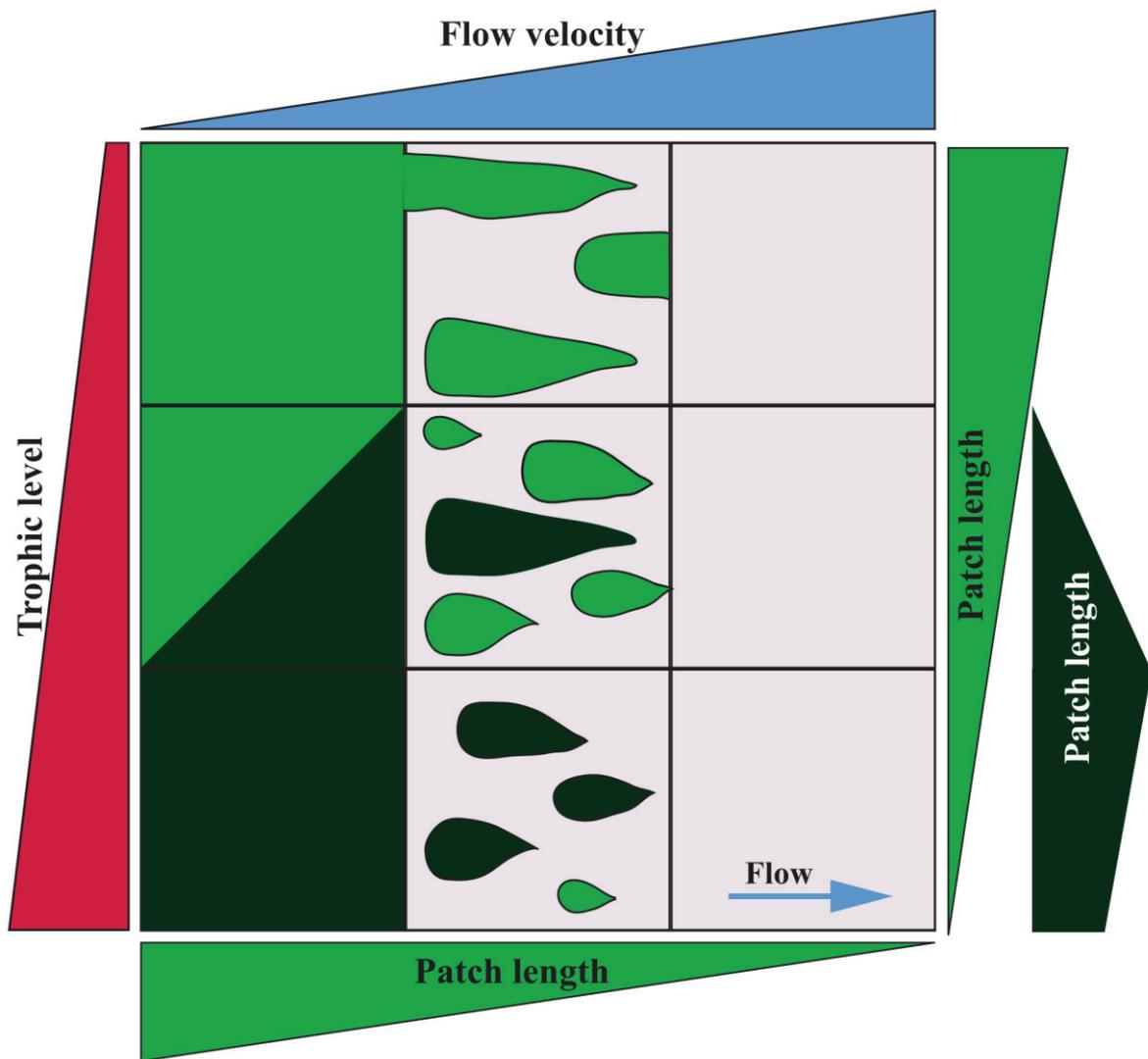


Fig. 8. A conceptual model of the effects of flow velocity and trophic level in lotic ecosystems for patch dynamics. The light green indicates vegetation typical of a system with low/intermediate trophic levels, while the dark green indicates the vegetation typical of more eutrophic conditions. At low velocities, the submerged plant can potentially cover the full bed, while for increasing flow velocity the scale-dependent feedbacks lead to patch formation. Extreme velocities impede the establishment of vegetation. The patch length for an oligotrophic/mesotrophic species should decrease with increasing mean flow velocity and increasing trophic level. For the more eutrophic species, the patch length should increase for increasing trophic level and decrease over a certain threshold.

6. Effects of patch size on the habitat modifications: consequences for the ecosystem functioning

Patches, in particular the ones over a certain size, reduce flow velocity resulting in increased water residence time and particle trapping. Hence, long patches act as biogeochemical hotspots (McClain *et al.* 2003), in which the accumulation of organic matter and nutrients supports certain microbiological processes, such as mineralisation and denitrification, that process and control the organic matter and nutrient loads in lotic system. For this reason, submerged plant patches play an important role in the nutrient cycles of lotic ecosystems, contributing to the capacity of “self-purification” of streams (Vincent and Downes 1980; Schulz *et al.* 2003).

The spatial self-organisation generated by the positive and negative feedbacks induced by plant aquatic patches, improves the heterogeneity of lotic systems (Palmer and Poff 1997; Sand-Jensen 1998). Firstly, plant patches increase the diversity of the physical habitats, generating areas with high and low flow velocities and coarse and fine sediments at the reach scale. Secondly, they also increase the biogeochemical diversity of sediments, with the succession of aerobic zones in bare sediment or small patches and anaerobic zones in long patches, hence influencing the microbiological processes and then the nutrient cycling, with possible cascading consequences on the productivity and biodiversity of streams (Dahm *et al.* 1987). Therefore the presence of different patch sizes, especially in reaches dominated by a single species, strongly contributes to the heterogeneity of the systems. Heterogeneity should also increase due to a higher biodiversity of submerged plant species with different traits, leading to a higher physical and biogeochemical diversity. Finally, patchiness has been demonstrated to increase the ecosystem resistance and resilience to disturbance (Rietkerk and van de Koppel 2008 and references therein). In the case of aquatic vegetation in lotic ecosystems, patchiness may increase plant resistance to mechanical damages induced by high discharge events by deviating flow nearby and above canopy patches (Schoelynck *et al.* 2012). The vegetation resisting high flow events by patchiness may retain part of the fine sediment and the microbial community of the system, assuring the resilience of the stream ecosystems in term of biogeochemical processes.

7. Evidence for niche construction?

Niche construction is defined as a process whereby organisms, through informed activities, modify their own and the population niches by affecting the selective pressures acting on them (Odling-Smee 1988; Odling-Smee *et al.* 2003; Odling-Smee *et al.* 2013). In lotic systems, submerged aquatic plants, acting as physical ecosystem engineers, modify their niches in terms of hydrodynamics and sediment characteristics, with consequences also for the biogeochemical characteristics. Feedbacks for plants depend on patch dimensions that regulate the intensity of the habitat modification. Submerged plants influence their own niches and the niches of their offspring not only by modifying the within-patch habitat conditions but also the surrounding conditions and in particular at the downstream edge of the patch. Indeed, patch expansion occurs by clonal multiplication mainly in the downstream direction, where compared to the upstream edge, hydrodynamic conditions are more favourable for plant growth and multiplication (Sand-Jensen and Madsen 1992; Schoelynck *et al.* 2017). By creating their own niche, aquatic plants mitigate the hydrodynamic pressures and the pressure related to the limiting nutrients. On the other side, the accumulation of phytotoxins can increase the selective pressure on aquatic plants and limit patch expansion (niche destruction). Niche construction and niche destruction together should induce the maintenance of a patchy state for submerged aquatic plants in lotic environment, preventing the system to shift into other states, as a bare bed or a bed fully covered by vegetation. Patchiness increases plant resistance to mechanical damages induced by high discharge events, by deviating flow principally next to patches (Schoelynck *et al.* 2012). Instead, in case of full vegetation cover, the flow is deviated above the canopies and, especially during high discharge events, canopies will tend to bend and flatten on the bottom, reducing the risk of uprooting but also protecting the bed from shear stress (Sand-Jensen and Pedersen 1999; Sand-Jensen 2003; Schoelynck *et al.* 2013). Prolonged high discharge could be still harmful to plants for the exposure to high velocities which still increase the risk of mechanical damage and uprooting (Schoelynck *et al.* 2013). Oppositely, a bare bed, in absence of submerged vegetation lacks many important functions for the ecosystems (Wetzel 1964; Pip and Robinson 1984; Lodge 1991; Sand-Jensen 1998; Wigand *et al.* 2001; Clarke 2002; Strayer and Malcom 2007).

PERSPECTIVES

My thesis improved the understanding of the role of patch size for the interactions of aquatic plants with hydrodynamics, sediment dynamics and nutrients. My finding improved the knowledge of the patch dynamics of submerged aquatic plants and the role of patch size for the functioning of the lotic ecosystems. However, many interesting questions on aquatic patches and their environmental interaction in lotic systems still need to be explored.

1. Effects of patch length on biogeochemical processes

My thesis investigated the effect of patch size on interstitial nutrient concentration and microbial respiration. To better understand the effect of patch length on the biogeochemical processes, other fundamental processes occurring in submerged aquatic patches that are important for nutrient cycling and patch growth should be measured. Litter is a fundamental source of carbon and nutrients for lotic systems (Mninsall 1967; Gulis and Suberkropp 2003). Aquatic patches act as a filter, trapping autochthonous and allochthonous detritus thus allowing microbial organism and macroinvertebrates to decompose them, therefore providing nutrients and energy for the system (Gregg and Rose 1982; Battle and Mihuc 2000; Gulis and Suberkropp 2003). It can be hypothesised that plant patches favour decomposition compared to bare area. However, this may depend on patch size, with small patches not being able to trap litter efficiently contrary to long patches. Measures of decomposition in bare areas and in patches of increasing sizes could quantify the role of plants patches and of their size in detritus decomposition. To quantify the effect of patch size on the microbial processes, the microbial activity and the microbial biodiversity could be also measured.

2. Role of plant traits and patch architectural characteristics

Natural submerged vegetation present in lotic systems has a high variety of morphologies and patch architectures, which influence in a different way both hydrodynamics and sediment characteristics (Sand-Jensen 1998; Sand-Jensen and Pedersen 1999). The differences in the modification of the physical habitat should induce different effects on the biogeochemical processes (Gutiérrez and Jones 2006). I already evocated the differences between plant species observed during the preliminary study of 2015, but further investigation should then focus on the effect of patch size on the biogeochemical processes for patches with different morphological and architectural characteristics and the consequent feedbacks for plants.

3. Feedbacks for plants: evidence for niche construction?

To better understand patch dynamics and the factors regulating patch growth, a long-term survey of patches of different sizes and measurements of patch downstream growth, on a longitudinal direction, would enable to estimate the plant fitness for patches of different sizes in different environmental conditions (*e.g.* increasing trophic level), individuating the presence of positive feedbacks and negative feedbacks for plants. Moreover, an experimental manipulation, such as fine sediment removal within plant patches, could help understanding the role of fine sediment accumulation for the presence of positive and negative feedbacks for plants.

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