Limnologica 43 (2013) 371–380

Contents lists available at SciVerse ScienceDirect

Limnologica

journal homepage: www.elsevier.com/locate/limno

Submerged macrophytes avoiding a negative feedback in reaction to hydrodynamic stress☆

Jonas Schoelynck[a,*,1], Dieter Meire[b,1], Kris Bal[a,d], Kerst Buis[a], Peter Troch[b], Tjeerd Bouma[c], Patrick Meire[a], Stijn Temmerman[a]

[a] University of Antwerp, Department of Biology, Ecosystem Management Research Group, Universiteitsplein 1C, B-2610 Wilrijk, Belgium
[b] Ghent University, Department of Civil Engineering, Hydraulics Laboratory, Sint-Pietersnieuwstraat 41, B-9000 Ghent, Belgium
[c] Netherlands Institute of Ecology, Centre for Estuarine and Marine Ecology, P.O. Box 140, 4400 AC Yerseke, The Netherlands
[d] University of Limpopo, Department of Biodiversity, PBag 1106, 0727 Sovenga, South Africa

ARTICLE INFO

Article history:
Received 22 October 2012
Accepted 15 May 2013
Available online 12 July 2013

Keywords:
Flume study
Erosion
Sedimentation
Bed shear stress
Scale-dependent feedbacks
Stream
Callitriche platycarpa

ABSTRACT

In most aquatic ecosystems, hydrodynamic conditions are a key abiotic factor determining species distribution and aquatic plant abundance. Recently, local differences in hydrodynamic conditions have been shown to be an explanatory mechanism for the patchy pattern of *Callitriche platycarpa* Kütz. vegetation in lowland rivers. These local conditions consists of specific areas of increased shear zones, resulting in additional plant stress and erosion of the sediment on the one hand and local decreased shear zones resulting in zones favourable to plant growth and sedimentation of bed material on the other hand. In this study, the process of this spatial plant-flow-sedimentation interaction has been illustrated quantitatively by *in situ* flume measurements. By disturbing the incoming discharge on a single patch in such flume, we have quantified the behaviour and influence of a *C. platycarpa* patch under normal field conditions (base flow). Additionally, the behaviour of a *C. platycarpa* patch under different conditions of hydrodynamic stress has been examined in a laboratory flume. Indeed, flexible, submerged macrophytes are capable to adapt patch dimensions with changing stream velocities. At times of modest hydrodynamic stress, the species takes a position near the water surface and optimises its leaf stand, thereby maximising its photosynthetic capacity. At times of peak discharge, the patch will bend down towards the river bed and become more confined and streamlined, as such averting the stream velocity and diminishing the risk of breaking or being uprooted.

In this paper, the processes of local hydrodynamic conditions on the patch and the patch' intriguing life strategy of avoiding negative feedback was shown.

Introduction

The interaction between macrophytes and the hydrodynamic regime in a stream has been a subject of research for over decades now. Part of this interest originates from hydraulic engineers interested in the way plants steer flow velocity patterns and water heights to give more accuracy to present-day models that are often exclusively based on (abiotic) river characteristics and physical laws (De Doncker et al. 2009). Others are interested how this diversity in flow patterns can influence the streams' ecology (Schoelynck et al. 2012b), geomorphology (Gurnell et al. 2010) or management (Bal and Meire 2009). Many studies have looked at this on a single-plant scale (Bal et al. 2011) or on uniformly distributed vegetation (Champion and Tanner 2000). However, the difficulty in studying the plant-flow interactions under natural conditions is compounded by the fact that plants often form patches, together with non-colonised spaces or spaces colonised by different types of vegetation (Sukhodolov and Sukhodolova 2010). That is why only few have studied patch behaviour *in situ* with changing discharges and stream velocities from an ecological point of view (Sand-Jensen and Pedersen 2008; Sand-Jensen and Pedersen 1999) or from a hydraulic engineering point of view (Sukhodolov and Sukhodolova 2010). Statzner et al. (2006) concluded that conventions, grounded on physical principles are strictly necessary for the characterisation of flow-plant interactions. However, sufficiently detailed data sets that would allow rigorous examination of flow-plant interactions relevant for natural conditions are still unavailable (Sukhodolov and Sukhodolova 2010). This paper is one of the first to address this scientific lacuna.

Recently, scale-dependent feedbacks have been shown to be an explanatory mechanism for the patchy pattern of *Callitriche*

☆ This article belongs to the special issue entitled 9th International Symposium on Ecohydraulics 2012.

[*] Corresponding author. Tel.: +32 3 265 22 52; fax: +32 3 265 22 71.
E-mail address: jonas.schoelynck@ua.ac.be (J. Schoelynck).

[1] These authors contributed equally.

0075-9511/$ – see front matter © 2013 Elsevier GmbH. All rights reserved.
http://dx.doi.org/10.1016/j.limno.2013.05.003

platycarpa Kütz. vegetation in lowland rivers (Schoelynck et al. 2012b); analogue to *Spartina anglica* C.E. Hubb patches on flood plains (Bouma et al. 2009; Temmerman et al. 2007; van Wesenbeeck et al. 2008). Spatial self-organisation of ecosystems is the process where large-scale ordered spatial patterns emerge from disordered initial conditions through local interactions between organisms and their environment; and has been demonstrated for many ecosystems (Rietkerk and Van de Koppel 2008). So-called scale-dependent feedbacks between organisms and their environment are often considered as a necessary condition for self-organised patchiness to form (Lejeune et al. 2004; Rietkerk and Van de Koppel 2008). The scale-dependent feedback principle implies that the presence of an organism has a positive feedback effect that is short-ranged (*i.e.* local facilitation through resource concentration or stress reduction) and a negative feedback effect that is long-ranged (*i.e.* inhibition in its surroundings by resource depletion or stress concentration). It was clearly shown that these habitat modifications have a short-range positive feedback on plant productivity on flood plains (van Wesenbeeck et al. 2008) and in freshwater rivers (Schoelynck et al. 2012b). Biomass slows down the current inside and in the immediate vicinity of vegetation patches, promoting the deposition of sediment and organic matter. This generally results in greater and deeper light penetration (Horppila and Nurminen 2003) and a higher nutrient availability (Brock et al. 1985; Webster and Benfield 1986). Alongside the patch, enhanced stream velocity can lead to erosion (Sand-Jensen and Mebus 1996). This can lead to a depletion of nutrient availability and an increase of physical disturbance (Sand-Jensen and Madsen 1992); hence a long-range negative feedback on plant productivity. This was shown on flood plains (van Wesenbeeck et al. 2008), but erosion could not be withheld as an explanatory factor in freshwater rivers, despite the clear presence of a negative feedback, proven with transplantation experiments (Schoelynck et al. 2012b).

This difference between intertidal *S. anglica* and freshwater river *C. platycarpa* may be explained by the difference in plant stiffness. The very stiff *S. anglica* is mostly emerged at times of peak discharges forcing all the water on flood plains to divert around the patch, leading to high flow velocities. Aquatic river vegetation is in general much more flexible and mostly submerged, so that water will tend to flow over it. This may result in more modest accelerations alongside the patches. It was therefore suggested that for aquatic river vegetation at base flow regimes, the proposed dynamics are most likely to be important but erosion is not the main negative feedback acting upon patch growth, but rather enhanced flow velocity and reduced sedimentation (Schoelynck et al. 2012b). Nevertheless, during high-discharge events, stream velocities can impose erosion around aquatic river vegetation patches (Sand-Jensen and Mebus 1996) and may govern drag and the probability of uprooting (Sand-Jensen and Pedersen 2008). Flow acceleration can be the most important stressor for *C. platycarpa* to grow (Riis and Biggs 2003; Riis et al. 2000). Subjected to a given current velocity, macrophytes experience a drag force 25 times higher than terrestrial plants exposed to a similar wind speed (Denny and Gaylord 2002). Biotic resistance is related with substrate stability or with low shear stress during stressful events (Lancaster and Hildrew 1993). Additionally, mechanical stress originating from hydrodynamic drag forces is a main structuring factor in aquatic vegetation communities (Biggs 1996; Spink and Rogers 1996).

In this current study, the interaction between a flexible submerged macrophyte patch of *C. platycarpa* and the hydrodynamic regime in a stream has been studied *in situ* as well as under laboratory conditions in order to understand the patch behaviour with changing stream velocities. *In situ* flume experiments are often used to study reach scale phenomenons (Gibbins et al. 2007; Schanz et al. 2002) and provide an excellent tool to work under the natural environmental conditions that are present in the studied ecosystem. It was preferred in the present study to measure the effect of plant-velocity interaction on turbulence, bed shear stress and hence possible erosion. By manipulating the incoming discharge, the existing equilibrium between velocity, bathymetry and vegetation becomes unbalanced, increasing the possibility to measure adequately critical zones of hydrodynamic stress. Laboratory flume tests are used to adequately measure changes in patch dimensions with changing incoming velocity. Changing patch characteristics may temper the magnitude of the effects in the critical stress zones. Hence, results of the laboratory flume experiments will help to understand field flume results. Against this background, the following research questions are addressed:

1) Where are the zones around a patch with a lower or higher stream velocity compared to incoming stream velocity?
2) Can we recognise specific critical zones near the patch edges with high turbulence values causing a risk of erosion, patch uprooting or stem breakage?
3) Do zones with enhanced or reduced stream velocity or turbulent stress correspond with zones of erosion or sedimentation respectively?
4) What is the importance of the free flowing zone above the patch in terms of averting incoming water and what is the consequence for the stream velocity alongside the patch?

This study is one of the first to integrate ecology and river hydraulics by performing *in situ* high resolution 3D-velocity measurements. Understanding and accurate prediction of transport processes in vegetative mosaics of fluvial ecosystems is a precondition for further developments in ecological modelling and can only be advanced through a series of case studies under natural conditions (Sukhodolov and Sukhodolova 2010).

Materials and methods

The *in situ* flume measurements were performed in September 2009 in the Zwarte Nete, a typical lowland river in the NE of Belgium. Water runs through a sandy river bed (median grain size $D_{50} = 167\,\mu\text{m}$) with an average stream velocity around $0.1\,\text{m}\,\text{s}^{-1}$ and an average discharge of $0.2\,\text{m}^3\,\text{s}^{-1}$ in September. The river study site is 4.5 m wide, water depth rarely exceeds 1 m and the water-surface slope is on average 0.12%. The aquatic vegetation comprises seven common true aquatic species but is dominated by *C. platycarpa* Kütz. growing in a mosaic pattern of distinct and confined patches, covering 20% of the river. It has a dense submerged biomass of flexible stems with small leaves. Stems can end in rosette shaped floating leaves surrounding flowers in spring.

A field flume was constructed around an average sized *C. platycarpa* patch (±1.2 m long, ±0.8 m wide, $115\,\text{g dry mass}\,\text{m}^{-2}$) at the beginning of the experiment. The patch canopy had an average inclination between 20° and 30° with the river bed and a free flowing space of minimum 0.10 m water was present above each patch. This results in a blockage area of 58% (definition by Green (2006): vegetated area in cross section divided by total cross section area). The field flume itself was 1.2 m wide and 10 m long and built from PVC coated sails attached to two rows of 11 wooden poles (See Fig. 1). The poles were anchored in the river bed at 1 m distance to each other. The first 2 m at the upstream part of the field flume (poles 1–3) were adjustable to be able to widen the inlet, and enhancing incoming discharge on day 2 of the experiment. The test section was 4.8 m long at the downstream end of the field flume (halfway pole 6 and 7–pole 11) with the *C. platycarpa* patch situated around poles 8–10 at the left bank side of the field flume and filling 75% of the flume's width. A free flowing section of 5 m between the end of the inlet and the beginning of the patch was