



Flow-velocity-dependent effects of turbid water on periphyton structure and function in flowing water

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Abstract

Land-use change, human activities, and dam management supply highly turbid water with high flow velocity; however, little is known about its effect on river ecosystems. Here, we studied the effects of flow velocity and suspended silt concentration on periphyton structure and function using experimental channels. The effects of flow velocity on algal biomass in the periphyton community depended on the suspended silt concentration; flow velocity decreased chlorophyll *a* in low concentrations of suspended silt (clear water), but not in moderate or high concentrations (turbid water). Filamentous cyanobacteria density was significantly influenced by flow velocity, whereas densities of non-filamentous cyanobacteria, green algae, and diatoms were not. Thus, flushing effects on attached algae, especially filamentous cyanobacteria, were exerted in clear but not in turbid waters, perhaps because algal assemblages were resistant to water current through the binding of large amounts of silt by extracellular polymeric substances. Inorganic matter and its ratio in the periphyton community decreased with flow velocity, but increased with suspended silt concentration, irrespective of flow velocity. Periphyton function, assessed by maximum photosynthesis rates and light-use efficiency, was influenced by flow velocity and suspended silt concentration through changes in periphyton structure. Flood events would be expected to refresh the periphyton community by removing senescent algae and deposited fine particles. However, we demonstrated that algae and silt in the periphyton community exposed to turbid waters with human-induced silt may accumulate, irrespective of flow velocity.

Keywords Chlorophyll *a* · Primary productivity · Sediment management · Self-shading · Silt-shading · Suspended silt

Introduction

River ecosystems have been altered due to land-use changes and human activities such as agriculture, forestry, mining, and urbanisation (Wood and Armitage 1997). One of the most pervasive influences on river ecosystems is the increase in fine sediment yield by accelerating land erosion (Waters 1995) and the rapid increase of turbidity in the water column during natural floods (Oeurng et al. 2011; Tamoooh et al.

2014). Additionally, most rivers have been dammed worldwide (Nilsson et al. 2005), and large amounts of fine sediment have been trapped in reservoirs (Morris and Fan 1998; Tiğrek and Aras 2011). To effectively manage the storage capacity of dam reservoirs, turbid water needs to be drained from the impoundments to downstream reaches (Kondolf et al. 2014). Sediment management is usually performed with large amounts of water such as floods to increase the discharge of deposited sediment (Liu et al. 2004; Kondolf et al. 2014). Then, considerable amounts of suspended particles, mainly silt and fine sand, are anthropogenically provided during natural and/or human-induced floods with high flow velocity.

The benthic periphyton community, in which algae are dominant members, is one of the most important primary producers in river ecosystems and the main food resource for many invertebrates and some fish, whereas their overproduction can deplete dissolved oxygen and alter hydraulics (Hynes 1970). The periphyton community has been used as a biological indicator of river health

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and anthropogenic effect (Stevenson 2014). Although the periphyton community is regulated by many factors, including light, nutrients, and grazing (Hynes 1970), the effects of turbid water are of great importance, because river turbidity is increased by human influence such as agriculture, forestry, urbanisation, and sediment management (Waters 1995; Davies-Colley et al. 1992). Suspended silt in turbid water can deposit on stone-surface periphyton, and siltation is retained after the transition from turbid to clear water (Graham 1990). Silt deposition can be partially removed by high flow velocity; however, some silt remains in the periphyton matrix, leading to changes in community structure (Flinders and Hart 2009).

Many studies have examined the effects of turbid water on the periphyton community, but most of them have been conducted in a relatively low to moderate flow velocity (i.e., $< 1 \text{ m s}^{-1}$), and showed that flowing silt adheres to periphyton surface (Jowett and Biggs 1997; Battin et al. 2003). However, turbid water with high suspended silt concentration usually has relatively high flow velocity during floods (Gordon et al. 2004; Liu et al. 2004; Asaeda and Rashid 2012). Since suspended particles can be infiltrated and intrude deeper into the matrix as flow velocity increases (Beschta and Jackson 1979; Schälchli 1992), a tight and solid periphyton matrix may be constructed by flowing turbid water with high suspended silt concentration and high flow velocity, likely leading to resistance to abrasion by water currents. Thus, we hypothesised that turbid water has flow-velocity-dependent effects on the periphyton community in flowing water. In fact, the periphyton community may be maintained in low flow velocity, in which the adherence of silt can increase in proportion to the increase in water turbidity. In comparison, the periphyton community may be removed by high flow velocity in clear water, whereas it may be more resistant in highly turbid water due to its silt-reinforced matrix. The effects of retained silt on the primary production of the periphyton community after the transition from turbid to clear water also remain unclear, although it is known that periphyton productivity decreases in turbid water due to light attenuation (Davies-Colley et al. 1992). Silt retained in the periphyton matrix may attenuate light availability to algae and hence decrease primary production, even in clear water. We examined the effects of flow velocity and suspended silt concentration on periphyton structure (i.e., algal biomass, retained inorganic and organic matter, and algal community structure) and function (i.e., maximum photosynthesis rates and light-use efficiency) by exposing periphyton community to different flow rates and different levels of turbidity in experimental channels.

Materials and methods

To examine the effects of flow velocity and suspended silt on the periphyton community, we conducted a study at the Aqua Restoration Research Centre (ARRC: Kawashima Kasada-machi, Japan) in September 2010 and 2012. Since the periphyton community changes temporally under natural conditions (Hill and Boston 1991), it was incubated at different developmental stages on ceramic tiles in an experimental stream at ARRC, within the basin of the Kiso River, Japan. We used the tiles and assessed the flow-velocity-dependent effects of turbid water on periphyton structure and function using recirculating experimental channels that can control flow velocity and suspended silt concentration (Fig. 1).

Experimental channels

We constructed six recirculating experimental channels using polyvinyl chloride (PVC) and stainless steel pipes (50 mm in diameter) as well as 200-L water tanks that were filled with 100 L of water obtained from the experimental stream at ARRC (Fig. 1). Stainless steel pipes were immersed in pools filled with ground water to reduce and maintain water temperature within the channels at 20–30 °C throughout the experimental period. The variation in water temperature within the channels was similar to that in the experimental stream (stream, $23.5 \pm 3.8 \text{ °C}$; channels, $23.2 \pm 4.5 \text{ °C}$). Some parts of the channels were constructed using clear pipes that allow light to pass through, and ceramic tiles (45 mm \times 45 mm \times 4 mm) were placed on

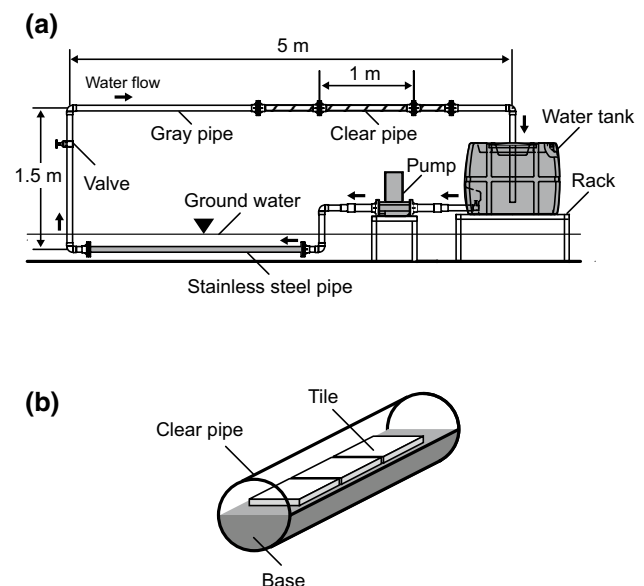


Fig. 1 A diagram of the experimental channel (a) and a close up of the clear pipe (b)

a semi-cylinder base (50 mm in diameter, 1 m in length; Fig. 1) within those areas. Water within the channels was circulated by pumps (65LPD6.15A; Ebara Corp., Japan) and was adjusted to provide a flow velocity of 0.5–4 m s⁻¹ using valves.

Experimental design

Ceramic tiles (MWO-T1; TILELIFE Inc., Japan) were used as standardised substrates (Hill and Boston 1991). The surface of the tiles resembled that of stone, and featured a slight and irregular roughness. Although periphyton community development depends on the substrate texture (Branco et al. 2010), periphyton community developed on the tiles as well as on natural cobble. A total of 800 tiles attached on PVC boards was anchored to a streambed reach of 100 m in the experimental stream (discharge = 200 L s⁻¹; mean water depth = 20 cm; mean flow velocity = 0.5 m s⁻¹), as described by Mochizuki et al. (2006). The streambed was covered by gravel, cobbles, and boulders, and was unshaded. The water in the experimental stream was brought in from the Shin-Sakai River, and the concentration of suspended solids in the experimental stream remained more or less stable throughout the experiment (less than 10 mg L⁻¹). Periphyton community changes dramatically within the first 2 weeks (McCormick and Stevenson 1991; Battin et al. 2003), and vulnerability to water current may depend on its development (Jowett and Biggs 1997). We incubated periphyton for 12 days and collected eight periphyton samples at 3, 6, and 12 days to assess successional changes; i.e., to evaluate at what point periphyton structure changed markedly. Incubation and sampling were repeated in tetraplicate.

Flowing turbid water due to human influence has large variations in flow velocity and suspended silt concentration during floods (Waters 1995; Morris and Fan 1998). Previous studies reported that the suspended silt concentration during flood events in Japanese rivers running through agricultural and deforested land is 10–10⁴ mg L⁻¹ (e.g., Kurashige et al. 2005; Sudo et al. 2009; Abe et al. 2014) and that turbid effluent water from dam reservoirs has a flow velocity of 2–8 m s⁻¹ and a suspended silt concentration of 10³–10⁵ mg L⁻¹ (Liu et al. 2004; Asaeda and Rashid 2012). We used a 2 × 3 × 3 completely randomised factorial arrangement to study the effects of two levels of flow velocity (0.5 and 4.0 m s⁻¹), three concentration levels of suspended silt (10, 1000, and 10,000 mg L⁻¹), and three development periods (3, 6, and 12 days) on periphyton structure. Because the concentration of suspended solids in the water obtained from the experimental stream was less than 10 mg L⁻¹ during the experiments in 2010 and 2012, the water was sieved with 63- μ m mesh to remove large particles and was used for the low concentration of suspended silt (10 mg L⁻¹). Moderate and high

concentrations (1000 and 10,000 mg L⁻¹) were prepared by adding kaolin (average particle size: 4.7 μ m, specific gravity: 2.6 g cm⁻³; Kanto Chemicals Co., Ltd., Japan) to the sieved water. Fluid density of turbid water was calculated as being 0.999 and 1.004 g cm⁻³ in moderate and high silt concentrations at 20 °C, respectively, and differed little from that of clear water (0.994 g cm⁻³).

At 3, 6, and 12 days after incubation in September 2010, we detached 48 randomly selected tiles from the PVC boards and placed them in the clear pipes of six channels (eight tiles per channel). Some studies have shown that effects of elevated flow velocity on removal of attached algae were observed within 1 h (Biggs and Thomsen 1995; Francoeur and Biggs 2006); if so, then short disturbance exposures may be sufficient to cause periphyton biomass removal. However, silt accumulation may increase after longer duration of flowing turbid water. The duration of turbid water due to natural flood events is highly variable, whereas human-induced flood events, such as water release from dams, are controlled, and may last from a few hours to a day or two (Koizumi et al. 2013). Hence, we exposed periphyton community to different flow rates and different levels of turbidity by operating the pumps for 24 h, and subsequently removed the tiles from the pipes and sampled the periphyton community. During operation of the pumps, small amounts of deposited silt (i.e., kaolin) were observed in the moderate and high concentration treatment tank, but the concentration of suspended silt remained more or less constant because of the stirring action of the current. The experiments were repeated in tetraplicate for each incubation period.

In addition, we used a 2 × 3 completely randomised factorial arrangement to study the effects of two levels of flow velocity (0.5 and 4.0 m s⁻¹) and three concentration levels of suspended silt (10, 1000, and 10,000 mg L⁻¹) on algal community structure and the photosynthesis-irradiance relationships of the periphyton community incubated for 12 d in September 2012. We used sealed recirculating chambers (Supplemental Material) filled with stream water to estimate photosynthesis-irradiance relationships (Dodds and Brock 1998; Hall et al. 2007). Four tiles were exposed to different treatments in the experimental channels for 24 h, and subsequently inserted into clear pipes in the recirculating chambers. Water in the chambers had a constant rate of about 0.5 m s⁻¹, and the temperature was kept constant by submerging the chambers in outside tanks filled with ground water. Photosynthesis-irradiance relationships were estimated by measuring diurnal dissolved oxygen (DO) and photosynthetic photon flux density (PPFD). The tiles were removed from the chambers after the 24 h study, and the periphyton community was sampled.

Periphyton structure

We measured five variables related to periphyton structure, including chlorophyll *a*, inorganic and organic matter content, inorganic ratio, and algal community structure. In September 2010, the periphyton community was scraped off using acrylate fibre cloths (Micro-cloth; Koyo Co. Ltd., Japan) that were dried at 60 °C (Mori and Saitoh 2014). Half of the cloths were placed in 99.5% ethanol at 5 °C for 24 h to extract pigments that were measured using a spectrophotometer (U-1500; Hitachi Co., Japan). Data were converted to chlorophyll *a* estimates (chl. *a*) as described by Hauer and Lamberti (2006). The remaining cloths were oven-dried at 60 °C and weighed to estimate the total mass of periphyton, including both organic and inorganic matter. Then, the cloths were ashed at 550 °C for 4 h and re-weighed. Burned residues of the cloths without periphyton were calculated in advance, and organic and inorganic contents were determined. The inorganic ratio was calculated by dividing the inorganic content by the total mass of periphyton.

In September 2012, the periphyton community was sampled using toothbrushes; this sampling technique differed from that used in 2010 for estimating algal community structure (Tanida et al. 1999; Hauer and Lamberti 2006). Each sample was placed in a vial and divided into three subsamples. Two subsamples were filtered through glass-fibre filters (Whatman GF/C; GE Healthcare UK Ltd., UK); one of them was exposed to ethanol for measuring chl. *a* (Hauer and Lamberti 2006), and the other was dried and ashed for estimating organic and inorganic matter contents. The third subsample was preserved in 5% buffered formalin solution and used to identify algae to the species or genus level. We grouped them into five morphological types (filamentous and non-filamentous cyanobacteria and green algae, and unicellular diatoms). We counted the number of filaments in filamentous cyanobacteria and that of cells in the four other types, and estimated their density (Hauer and Lamberti 2006).

Periphyton function

To estimate periphyton function, photosynthesis-irradiance relationships were modelled by fitting the DO and PPFD data into the two-parameter hyperbolic tangent equation (Jassby and Platt 1976):

$$P = P_{\max} \tanh(\alpha I / P_{\max}) \quad (1)$$

where *P* is the instantaneous photosynthetic rate at a given PPFD represented by *I*; P_{\max} is the estimated maximum rate; α is the slope of the initial part of the relationship, representing light-use efficiency (Zheng et al. 2015). *P* was calculated based on diurnal DO changes, and both P_{\max} and α were

estimated by the means of least-squares nonlinear regression (Beaulieu et al. 2013). Previous studies have noted the importance of distinguishing between biomass-specific and area-specific community function, because algal density has different effects (Stevenson et al. 1996). Area-specific function probably increases with increase in algal biomass on substrates whereas biomass-specific function most likely decreases because resource (light and nutrient) availability normally decreases as algal density increases (Stevenson 1990). P_{\max} and α were then calculated for the unit of substratum area (P_{\max}^{area} and α^{area}) and chl. *a* ($P_{\max}^{\text{chl. } a}$ and $\alpha^{\text{chl. } a}$).

Statistical analysis

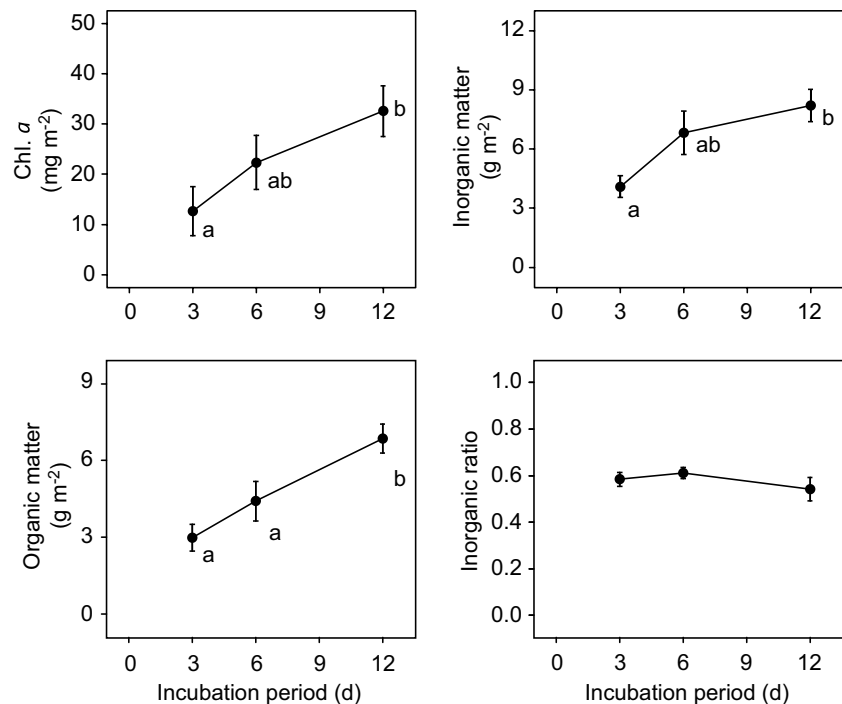
To assess successional changes in the four variables of periphyton structure (chl. *a*, inorganic and organic matter contents, and inorganic ratio), one-way analysis of variance (ANOVA) was performed in conjunction with Tukey's honestly significant difference (HSD) test. To examine the effects of flow velocity, suspended silt concentration, and development period on chl. *a*, inorganic and organic matter, and inorganic ratio that were obtained in 2010, we used three-way ANOVA in conjunction with Tukey's HSD test, when any interaction effects of the three variables were significant. Likewise, to estimate the effects of flow velocity and suspended silt concentration on algal community structure (i.e., density of each morphological group) and the four variables of periphyton function (P_{\max}^{area} , α^{area} , $P_{\max}^{\text{chl. } a}$, and $\alpha^{\text{chl. } a}$) that were obtained in 2012, we conducted two-way ANOVA in conjunction with Tukey's HSD test. We also performed multiple regression analysis to elucidate any relationships between periphyton function and structure. When the results of two-way ANOVA showed a significant interaction effect, we conducted multiple regression analysis in low and high flow velocity, because variation in periphyton function was considered to be related to different periphyton structures. All analyses were performed using the R environment for statistical computing (R Development Core Team, Vienna, Austria) with nls (Bates and Chambers 1992) and car (Fox and Weisberg 2011). Logarithmic transformations were performed for inorganic matter to standardise variances. All data in the present study were included in Supplementary Table.

Results

Periphyton development

Periphyton structure varied throughout the incubation period (Fig. 2); the incubation time significantly affected chl. *a* and inorganic and organic matter (one-way ANOVA, $F_{2,9} = 4.46\text{--}9.70$, $P = 0.006\text{--}0.05$), but not the inorganic ratio ($F_{2,9}$

Fig. 2 Temporal changes in chl. *a*, inorganic and organic matter contents, and inorganic ratio of periphyton. Data are shown as mean \pm standard error. Different letters show significant differences at $P < 0.05$



= 1.17, $P = 0.35$). Both chl. *a* and inorganic matter were different between 3 d and 12 d after incubation (Tukey's HSD test, $P = 0.01$ – 0.05), while organic matter significantly varied between 3 or 6 days and 12 days after incubation (Tukey's HSD test, $P = 0.004$ – 0.05).

Periphyton structure

Flow velocity, suspended silt, incubation time, and velocity \times suspended silt interaction had significant effects on chl. *a*. (Table 1), showing that the effect of flow velocity on chl. *a* depended on the suspended silt concentration (Fig. 3). Flow velocity decreased chl. *a* in low concentrations of suspended silt (10 mg L^{-1}), but not in moderate or high concentrations (1000 and $10,000 \text{ mg L}^{-1}$). Only chl. *a* exposed to a low suspended silt concentration with high velocity was significantly lower than that exposed to other conditions (Fig. 3). Inorganic matter and its ratio were influenced by flow velocity, suspended silt, and incubation time, whereas their interactions were not significant (Table 1). Both variables decreased with flow velocity and increased with the suspended silt concentration (Fig. 3). However, inorganic matter, but not the inorganic ratio, increased with incubation time (Table 1). The effects of flow velocity and incubation time on organic matter were significant, whereas those of suspended silt and their interactions were not significant (Table 1). Organic matter decreased with flow velocity and increased with incubation time (Table 1; Fig. 3).

In the algal community, filamentous cyanobacteria density was significantly influenced by flow velocity (two-way

ANOVA, $F_{1,18} = 4.46$, $P = 0.05$, Fig. 4), but not by suspended silt concentration ($F_{2,18} = 1.83$, $P = 0.19$) and their interaction ($F_{2,18} = 1.05$, $P = 0.37$). None of the three variables had any significant effects on non-filamentous cyanobacteria, filamentous and non-filamentous green algae, and unicellular diatom densities ($P = 0.12$ – 0.69 , Fig. 4).

Periphyton function

Flow velocity negatively affected $P_{\text{max}}^{\text{area}}$ (two-way ANOVA, $F_{1,14} = 4.70$, $P = 0.05$, Fig. 5), but not α^{area} ($F_{1,14} = 1.17$, $P = 0.30$, Fig. 5), whereas both variables were unrelated to suspended silt or their interactions ($F_{2,14} = 0.46$ – 1.00 , $P = 0.22$ – 0.45). $P_{\text{max}}^{\text{chl. } a}$ was significantly affected by the interaction of flow velocity and suspended silt ($F_{2,14} = 8.33$, $P < 0.01$), and it was considerably higher in a low suspended silt concentration and high flow velocity compared with other conditions (Fig. 5). Furthermore, it did not differ among different concentrations of suspended silt in low flow velocity, and it decreased with the increasing concentration of suspended silt in high flow velocity (Fig. 5). Additionally, $\alpha^{\text{chl. } a}$ was associated with flow velocity ($F_{1,14} = 5.76$, $P = 0.03$) and suspended silt ($F_{2,14} = 7.06$, $P < 0.01$), but not their interaction ($F_{2,14} = 2.92$, $P = 0.09$); it was lower in low flow velocity than in high flow velocity (Fig. 5) and was higher in a low suspended silt concentration (10 mg L^{-1}) than in a high concentration ($10,000 \text{ mg L}^{-1}$).

Multiple regression analysis showed that $P_{\text{max}}^{\text{area}}$ significantly increased with chl. *a* but was not related to inorganic or organic matter (Table 2). In addition, α^{area} significantly

Table 1 Effects of flow velocity, concentration of suspended silt (SS), incubation period, and their interactions on chl. *a*, inorganic and organic matter, and inorganic ratio of periphyton

Response variables	Flow velocity		Suspended silt (SS)		Incubation period		Velocity × SS		Velocity × period		SS × period		Velocity × SS × period	
	<i>P</i>	Results of MC	<i>P</i>	Results of MC	<i>P</i>	Results of MC	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>
Chl. <i>a</i>	<0.01	–	<0.01	–	<0.001	3 ^a , 6 ^b , 12 ^c	<0.01		0.22		0.47		0.14	
Inorganic matter	<0.001	Low ^a , High ^b	<0.001	10 ^a , 1000 ^b , 10000 ^c	<0.001	3 ^a , 6 ^{ab} , 12 ^b	0.79		0.42		0.79		0.95	
Organic matter	<0.001	Low ^a , High ^b	0.70	–	<0.001	3 ^a , 6 ^b , 12 ^c	0.60		0.14		0.97		0.99	
Inorganic ratio	<0.001	Low ^a , High ^b	<0.001	10 ^a , 1000 ^b , 10000 ^c	<0.001	3 ^a , 6 ^b , 12 ^a	0.62		0.15		0.76		0.92	

MC, multiple comparisons using Tukey's honest significant difference (HSD) test
 Different superscript letters show significant differences at the corresponding *P* level

decreased and increased with inorganic matter and organic matter, respectively (Table 2), but it was not related to chl. *a* (Table 2). The relationships between $P_{\max}^{\text{chl.}a}$ and periphyton structure depended on flow velocity (Table 2). $P_{\max}^{\text{chl.}a}$ was not associated with periphyton structure in low flow velocity, but decreased with chl. *a* in high flow velocity, whereas $\alpha^{\text{chl.}a}$ decreased with chl. *a* and inorganic matter and increased with organic matter (Table 2).

Discussion

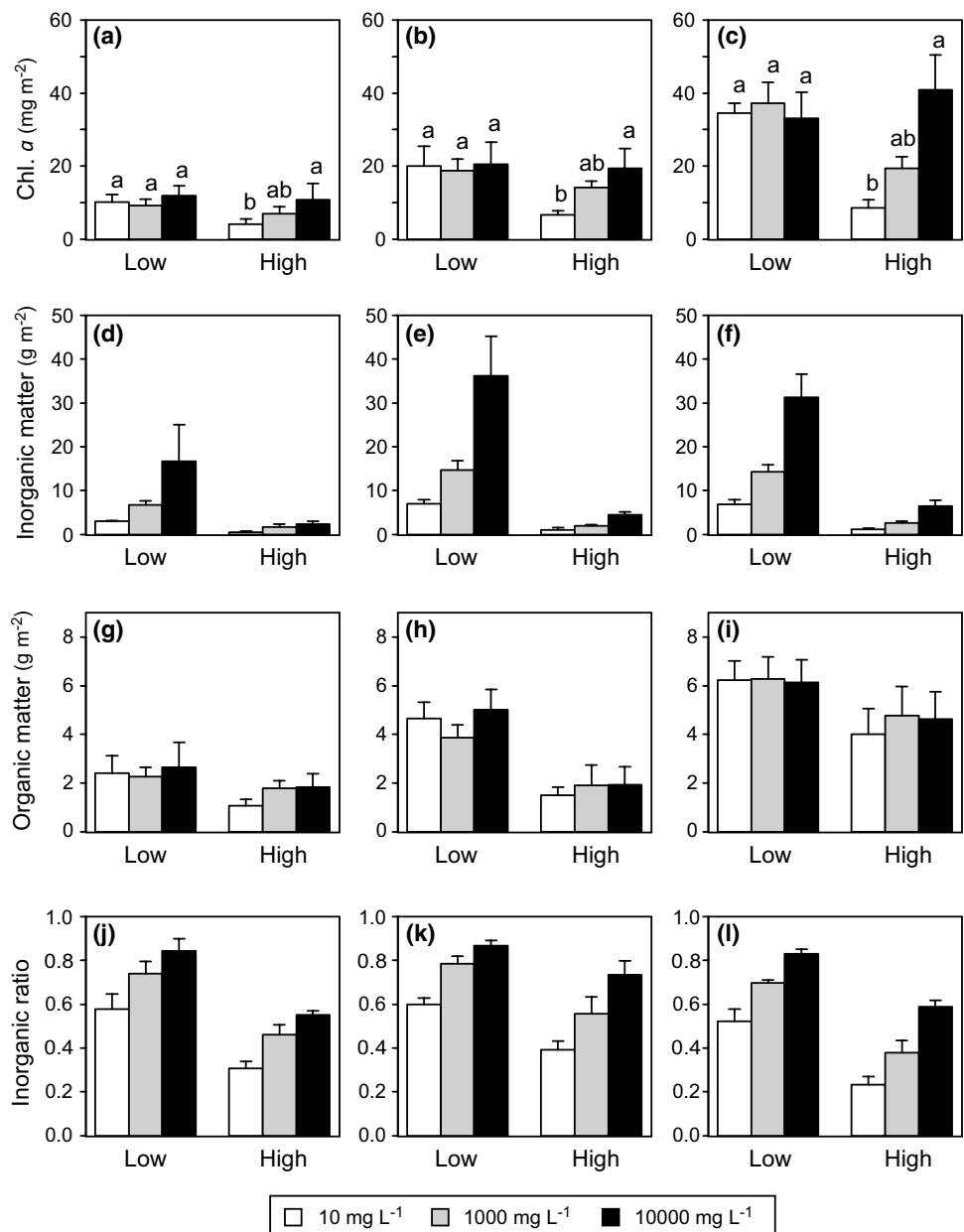
Periphyton development

Periphyton structure incubated in an experimental stream was similar to that in the vicinity of the basin (Takao et al. 2008; Miyake et al. 2012) and gradually changed over 12 days (Fig. 2). This trend is often observed in hydrologically stable rivers (Hill and Boston 1991; Wellnitz and Rader 2003). The growth of attached algae in the periphyton community increased chl. *a* (Fig. 2), contributed to the retention of suspended particles (Battin et al. 2003), and incrementally increased inorganic and organic matter contents (Fig. 2). However, the inorganic ratio did not vary with incubation time, since both inorganic and organic matter contents showed similar changes. Incubation time significantly influenced chl. *a* and inorganic and organic matter contents (Fig. 2); however, all interaction effects with incubation time were insignificant for all four variables of periphyton structure (Table 1). Thus, the effects of flow velocity and suspended silt concentration on periphyton structure were similar in each developmental stage (Fig. 3) and hence, the following discussion can be applied for all incubation periods in the present study.

Periphyton structure

The effects of flow velocity on algal biomass in the periphyton community depended on the suspended silt concentration (Fig. 3). Periphyton community may develop within a hydrodynamic boundary layer where frictional forces between water and substratum slow water flow (Silvester and Sleigh 1985; Losee and Wetzel 1993). However, fluids moving past objects attached to a surface produce a shear stress that is a function of current velocity and fluid density (Gordon et al. 2004), and several studies have shown that attached periphyton can be dislodged by shear stress imposed by elevated velocity (Cardoso-Leite et al. 2015). Herein, algal biomass decreased with flow velocity in clear running water (Fig. 3), demonstrating that high flow velocity (i.e., 4.0 m s⁻¹) can remove the attached algae through current-induced shear stress. Moreover, algal morphological characteristics are associated with vulnerability to

Fig. 3 Effects of flow velocity and suspended silt concentration on periphyton structure at 3 days (**a, d, g, j**), 6 days (**b, e, h, k**), and 12 days (**c, f, i, l**) after incubation. Data are shown as mean \pm standard error. Different letters show significant differences at $P < 0.05$

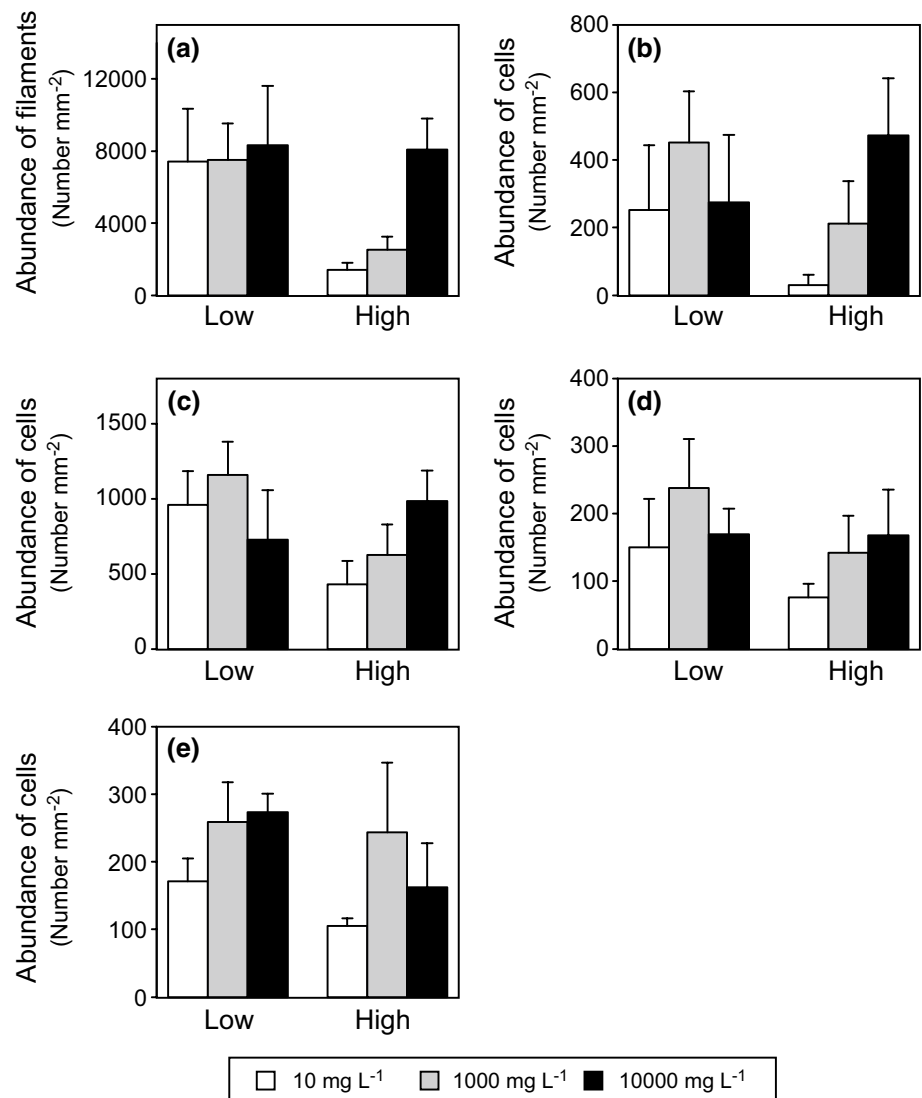


shear stress (Tonetto et al. 2014). Shear force enhanced by increasing flow velocity affects larger algae, such as filamentous species, because smaller ones may lie deeper within the boundary layer (Silvester and Sleight 1985; Graba et al. 2013). Thus, the filamentous cyanobacteria that dominated in periphyton community may decline with flow velocity as they expand out of the boundary layer, thereby increasing their susceptibility to shear stress (Steinman and McIntire 1990; Schneck and Melo 2012).

Algal biomass was not significantly different between low and high flow velocity treatments in moderately and highly turbid water, and it was higher in highly turbid water with high flow velocity than in clear water with high flow velocity (Fig. 3). These results suggested that erosion of algal

biomass may not be exerted as strongly in turbid running water. However, previous studies have indicated that flowing sediment enhances the removal of periphyton biomass in experimental flow increases (e.g., Horner et al. 1990) and natural floods (e.g., Luce et al. 2013). These contradictory results could be attributed to differences in sediment texture and the grain size distribution of turbid water. Shear force for attached periphyton can be enhanced by increasing fluid density (Gordon et al. 2004; Cardoso-Leite et al. 2015), but differences in fluid density between clear and turbid water are generally slight, except for debris flow. Direct abrasion by sediment load in turbid water may therefore be more important for removal of periphyton community (Luce et al. 2013), but the removal force depends on grain size. Saltating

Fig. 4 Effects of flow velocity and suspended silt concentration on the number of filaments in filamentous cyanobacteria (a) and that of cells in non-filamentous cyanobacteria (b), filamentous (c) and non-filamentous (d) green algae, and unicellular diatoms (e). Data are shown as mean \pm standard error



coarse particles abrade surfaces more effectively than do fine particles travelling primarily in suspension (Luce et al. 2013), because suspended particles have less frequent contact with the streambed, where periphyton community develops, than do saltating particles (Dade and Friend 1998). Furthermore, the kinetic energy of impact increases with increasing grain size (Lamb et al. 2015). Here, we focused on the effects of silty turbid water, because this is the form most associated with human influence (e.g., agriculture and sediment management in dam reservoirs). Because flowing silt moves primarily in suspension (Gordon et al. 2004), its abrasive force may be extremely small. Turbid water in natural flood events contains various sediment size. Thus, the characteristics of turbid water likely modulate the effects on periphyton.

The abrasion effects of running water on attached algae may be weakened in highly turbid water with high flow velocity, because silt might enter deep into the periphyton

community and become closely connected to algae by extracellular polymeric substances (EPS). EPS can couple algae with fine particles, creating algal assemblages with increased resistance to erosion and mobilisation (de Brouwer et al. 2005; Gerbersdorf et al. 2008). Van de Koppel et al. (2001) showed that the benthic algal community has higher resistance to erosion in tidal flat with silt compared with that with sand, because community cohesion is enriched by the close connection with silt due to secreted EPS. In addition, some particles that cannot accumulate on the surface of the periphyton community might enter deep into the community in high flow velocity (Beschta and Jackson 1979; Schälchli 1992). In the present study, filamentous cyanobacteria were influenced by flow velocity and suspended silt concentration (Fig. 4), and variations were comparable to those in chl. *a* (Fig. 3). Interwoven matrices of filamentous cyanobacteria are resistant to disruption by scour (Stevenson et al. 1996). Then, the layer of filamentous cyanobacteria possibly

Fig. 5 Effects of flow velocity and suspended silt concentration on periphyton photosynthetic attributes. Data are shown as mean \pm standard error. Different letters show significant differences at $P < 0.05$

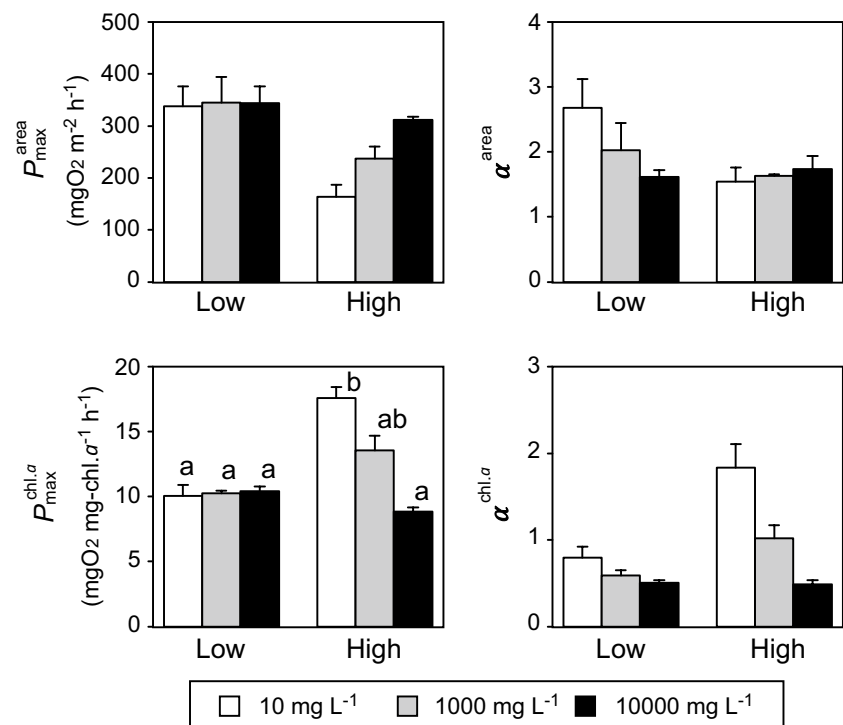


Table 2 Multiple regression analysis of periphyton function (P_{\max}^{area} , α^{area} , $P_{\max}^{\text{chl.}a}$, and $\alpha^{\text{chl.}a}$) and structure (chl. a , inorganic and organic matter contents)

Dependent variables	Flow velocity	F	P	Intercepts	Chl. a			Inorganic matter			Organic matter		
					Coef.	t	P	Coef.	t	P	Coef.	t	P
P_{\max}^{area}	–	25.37	<0.001	68.00	7.82	5.49	<0.001	–57.4	–1.47	0.16	12.79	0.69	0.50
α^{area}	–	6.37	<0.01	0.30	0.01	0.59	0.57	–1.38	–2.92	0.01	0.65	2.91	0.01
$P_{\max}^{\text{chl.}a}$	Low	0.14	0.93	–	–	–	–	–	–	–	–	–	–
	High	21.46	<0.01	16.24	–0.23	–3.13	0.02	–7.90	–1.56	0.17	1.92	1.41	0.21
$\alpha^{\text{chl.}a}$	–	14.67	<0.001	0.12	–0.004	–4.62	<0.001	–0.08	–3.10	<0.01	0.04	3.36	<0.01

Coef., coefficient in multiple regression model

P_{\max} and α were estimated by the means of least-squares nonlinear regression

P_{\max} and α were calculated for the unit of substratum area (P_{\max}^{area} and α^{area} , respectively) and chl. a ($P_{\max}^{\text{chl.}a}$ and $\alpha^{\text{chl.}a}$, respectively)

became more resistant to water current through the binding of large amounts of silt, leading to the inhibition of algal abrasion by reinforcing effects.

Silt accumulation (estimated as inorganic matter) in the periphyton community increased with suspended silt concentration and decreased with flow velocity (Fig. 3). The settling velocity of silt is extremely low (Morris and Fan 1998), and then it usually deposits only in marginal and pool areas and not in runs or riffles (Hynes 1970). However, silt accumulation was observed not only in low (0.5 m s^{-1}), but also in high (4.0 m s^{-1}) flow velocity treatments (Fig. 3). These results were consistent with previous studies, which showed that fine particles could be entrapped in the mucilaginous surfaces of the periphyton community in runs and riffles

(Graham 1990; Yamada and Nakamura 2002). Nevertheless, silt accumulation was greater in low than in high flow velocity (Fig. 3), indicating that the accumulation could be reduced proportionally to flow velocity. The interruption of silt accumulation by water with high flow velocity may be provided through two processes: (1) decrease in the retention of inorganic matter relating to algal biomass (Battin et al. 2003) and (2) inhibition of flowing silt adherence to periphyton surface by water current with high flow velocity (Flinders and Hart 2009). In the present study, chl. a and inorganic matter declined in clear water with high flow velocity (Fig. 3), revealing that water with high flow velocity could detach already deposited inorganic particles as well as algae. Additionally, algal biomass exposed to turbid water

was not influenced by flow velocity, but inorganic matter was less in high than in low flow velocity (Fig. 3), showing that high flow velocity could restrict the additional silt accumulation in the periphyton community. Previous studies showed that silt entrapment in the periphyton community increases the inorganic ratio (Eloranta and Kunnas 1979; Cline et al. 1982). In the present study, the inorganic ratio was influenced by flow velocity and suspended silt concentration, similarly to inorganic matter (Fig. 3), and thus, variations in the inorganic ratio may be affected by the degree of silt accumulation in the periphyton community.

Effect on photosynthesis

Periphyton function was influenced by flow velocity and suspended silt concentration through changes in its structure. Area-specific maximum photosynthesis rates, P_{\max}^{area} , increased with algal biomass (Table 2), and thus, the variation was almost identical to that in the biomass (Figs. 3, 5). Many studies have reported positive relationships between P_{\max}^{area} and algal biomass; for example, P_{\max}^{area} can be enhanced by an increase in chl. *a* associated with periphyton development (Hill and Boston 1991). In the present study, P_{\max}^{area} was not influenced by suspended silt, whereas chl. *a* was associated with silt in high flow velocity (Table 1). These results showed that the density of turbid water might indirectly influence P_{\max}^{area} through algal biomass in high flow velocity. Area-specific light-use efficiency, α^{area} , was negatively and positively related to inorganic and organic matter, respectively (Table 2), but not associated with flow velocity and suspended silt concentration (Fig. 5). Since inorganic and organic matter contents were negatively influenced by flow velocity, but had opposite effects on, flow velocity probably did not affect α^{area} . Although the different concentrations of suspended silt in high flow velocity caused moderate variation in inorganic matter (Fig. 3), it did not have any effect on α^{area} . The negative relationship between inorganic matter and α^{area} showed that periphyton covered by accumulated silt might need more PPFD in order to attain the maximum level of algal productivity (i.e., silt-shading). Although many studies have shown that suspended silt has negative effects on algal productivity by preventing light penetration into the water (Davies-Colley et al. 1992), we demonstrated that accumulated silt determined algal productivity. Since α^{area} increased with organic matter (Table 2), non-algal organisms might positively mediate algal productivity in relatively low-light conditions.

The individuals growing deeper within an algal community receive less light, and productivity is restricted when densely accumulated algae pile within a limited space (Hill and Boston 1991). At that point, biomass-specific maximum photosynthesis rates, $P_{\max}^{\text{chl. } a}$, may be restricted by algal self-shading, although we did not estimate vertical profiles of

dissolved oxygen and light availability in periphyton community (Nakano et al. 2006). In high flow velocity, algal biomass was the only factor that affected $P_{\max}^{\text{chl. } a}$ (Table 2), likely leading to the highest value in the absence of algal self-shading (Fig. 5). Additionally, biomass-specific light-use efficiency, $\alpha^{\text{chl. } a}$, was influenced by flow velocity and suspended silt concentration through the three periphyton structure variables, namely chl. *a*, inorganic matter, and organic matter. Periphyton structure had different effects on $\alpha^{\text{chl. } a}$, due to the opposing relationships of inorganic and organic matter contents and the negative effect of chl. *a*. Then, $\alpha^{\text{chl. } a}$ was higher after high flow velocity than after low flow velocity, probably due to chl. *a*. The effects of suspended silt on $\alpha^{\text{chl. } a}$ could be interpreted by the negative relationship between inorganic matter and $\alpha^{\text{chl. } a}$ (Table 2), showing that not only α^{area} , but also $\alpha^{\text{chl. } a}$, were restricted by silt-shading. Additionally, since algal self-shading was considered very low in clear water with high flow velocity, $\alpha^{\text{chl. } a}$ was the highest under these conditions. These results showed that most algae could immediately attain the maximum level of their inherent photosynthetic capacity in clear running water with high flow velocity. Therefore, biomass-specific photosynthesis-irradiance relationships were determined by flow velocity and silt concentration, probably through algal self-shading and shading by silt.

Periphyton supports river food webs, and its structure and function affect river ecosystems. An increase in the inorganic ratio due to silt accumulation can reduce the availability of food resources to the periphyton consumers (Peeters et al. 2006). The combination of high biomass and high productivity of algal assemblages may lead to overgrowth and a greater proportion of senescent algae, both of which frequently decrease species diversity in animal assemblages (Stevenson et al. 1996). Natural and human-induced floods are expected to refresh periphyton community by removing both deposited inorganic matter and attached senescent algae (Arthington 2012). In the present study, silt accumulation decreased with increases in flow velocity, but the amount and ratio of inorganic matter increased with increases in the concentration of suspended silt, regardless of flow velocity. Additionally, higher algal biomass and productivity were maintained in the periphyton community exposed to turbid water with high flow velocity. Therefore, our findings suggested that the flood water containing considerable concentrations of suspended particles, mainly silt and fine sand, that typically result from human activities might be insufficient for refreshing periphyton community even in high flow velocity. The possibility of algal remains and silt accumulation in periphyton community exposed to turbid waters with human-induced silt should be considered for the prevention of river ecosystem degradation. For river conservation and management, periphyton-turbidity relationships should be explored in more detail. We used turbid water dominated by

silt due to human influence, but did not examine the wide variation in grain size distribution. Since we incubated periphyton for 12 days, our findings are limited to the relatively early stages of periphyton development. Thus, future studies need to investigate influence of the grain size distribution and successional stage in combination with the flow velocity and suspended silt concentration to clarify the effects of turbid water on the periphyton community.

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