PRIMARY RESEARCH PAPER

The flow velocity as driving force for decomposition of leaves and twigs

André Luiz dos Santos Fonseca · Irineu Bianchini Jr. ·
Cristiane Marques Monteiro Pimenta ·
Cássio Botelho Pereira Soares · Norberto Mangiavacchi

Abstract The water velocity and associated physical forces affect the distribution of organisms in rivers and streams; changes in the flows can also affect the organic matter decomposition and transport of detritus in lotic systems. The main objective of this study was to evaluate (120 days) the effects from the water flow velocity on the mass loss of leaves and stems in artificial channels (at $24 \pm 1.0°C$; current velocities: 0, 5, and 10 cm s^{-1}). The kinetic model used suggested that in addition to abrasion, the velocity of flow stressed the detritus fibers altering the decomposition pathways. Overall, the changes in the kinetic parameters varied linearly with the increase in flow velocity. Weight losses of the leaves were more affected by the flow velocity than those of the twigs. However, abrasion was more effective in the twigs than that in the leaves detritus. In the lotic systems, the leaves have greater importance in the detritus chains in the short term and in the conditions of backwater. The boost of flow velocity tends to change the refractory fractions (RPOM) into more labile/soluble compounds and increase the values of RPOM rate constant, owing to abrasion.

Keywords Abrasion · Aerobic decomposition · Plant debris · Mathematical model · Lotic systems

A. L. dos Santos Fonseca
Instituto Federal de Educação, Ciência e Tecnologia do
Rio de Janeiro, Rua Carlos Wenceslau, 343, Rio de
Janeiro, RJ CEP 21715-000, Brazil

A. L. dos Santos Fonseca · I. Bianchini Jr.
Programa de Pós-Graduação em Ecologia e Recursos
Naturais, Universidade Federal de São Carlos, Rodovia
Washington Luiz, km 235, CP 676, São Carlos,
SP CEP 13565-905, Brazil

I. Bianchini Jr. (✉)
Departamento de Hidrobiologia, Universidade Federal de
São Carlos, Rodovia Washington Luiz, km 235, CP 676,
São Carlos, SP CEP 13565-905, Brazil
e-mail: irineu@ufscar.br

C. M. M. Pimenta · N. Mangiavacchi
Grupo de Ensaios e Simulações Ambientais em
Reservatórios, Universidade Estadual do Rio de Janeiro,
Rua Fonseca Teles, 121, Rio de Janeiro,
RJ CEP 20940-903, Brazil

C. B. P. Soares
Furnas Centrais Elétricas, Rua Real Grandeza, 219, Rio de
Janeiro, RJ CEP 22281-900, Brazil

Introduction

In many countries, a significant contribution of the energy is derived from hydroelectricity, and several hydroelectric power plants are now under construction or being planned. The anthropic river manipulation promotes social benefits, but it can damage or eliminate ecosystem services (Richter et al., 2006). Under natural condition, the variations of the water flow interact with the underlying geology, shaping the

physical and chemical patterns on which the biological communities have developed over long periods of time (Ward, 1998; Lytle & Poff, 2004). When the natural flow of water is modified, changes occur in the patterns of material transport, availability of resources, succession and death of plants, and composition of biological communities, thus altering the ecosystem services (Naiman et al., 2008).

The water flow in streams and rivers is an important variable (Power et al., 1995, Walker et al., 1995), which shapes ecological properties such as biodiversity and ecosystem functioning (Hart & Finelli, 1999; Bunn & Arthington, 2002; Poff et al., 2007). Most of the changes in natural flows result from dams and impoundments (Poff & Zimmerman, 2010) to meet the need for water, energy, and transport (Nilsson et al., 2005); in the world, there are more than 500,000 large water reservoirs (Downing et al., 2006). Changes in magnitude, frequency, and time in natural flows affect the ecological characteristics on a global scale (Nilsson et al., 2005, Poff et al., 2007). Upstream and downstream changes in dams are caused by flood, flow manipulation, and habitat fragmentation (Humborg et al., 1997; Jansson et al., 2000; Nilsson & Berggren, 2000), leading to a reduction in variabilities of the habitat and the species diversity. The composition of macroinvertebrate and fish communities may then be altered (Bunn & Arthington, 2002).

Decomposition has been used as a measure of functional integrity in streams (Gessner & Chauvet, 2002; Death et al., 2009; Sandin & Solimini, 2009). The main energy source for food webs in streams is allochthonous organic matter from terrestrial vegetation (Cummins et al., 1989; Wallace et al., 1997; Abelho, 2001). In water, the decomposition of allochthonous organic matter starts immediately and usually occurs in three overlapping phases: (1) leaching of soluble compounds, which can lead to loss of approximately 42% of the initial mass of the leaves detritus (Abelho, 2001); (2) decomposition by microorganisms, which may be responsible for the loss of ca. 27% of the mass of leaves mass (Hieber & Gessner, 2002); and (3) biological and physical fragmentations. Fragmentation results from the biological activity of invertebrates (Graça, 2001), which can result in 64% of weight loss (Hieber & Gessner, 2002). In the studies that address the organism's activity during decomposition, the role of physical fragmentation has been little explored, but is usually related to the water

regime, particularly the velocity of water flow (Gessner et al., 1999; Lepori et al., 2005; Paul et al., 2006). The flow of water may vary spatially (Naiman et al., 2008), and therefore the results of decomposition studies can be influenced by the location of the detritus (Ferreira et al., 2006). In addition, decomposition rates depend not only on the velocity and turbulence of the current but also on the detritus resistance (Abelho, 2001; Lecerf & Chauvet, 2008). If abrasion determines the rates, then the less tough debris decomposes faster (Molinero et al., 1996). This issue can be addressed by isolating the effect of the flow velocity using an artificial channel (flume) where the current velocity can be controlled (Ferreira et al., 2006).

A quantitative relationship between the change in water flow and the ecological responses is usually difficult to establish (Poff & Zimmerman, 2010). Nevertheless, changes of flow are known to affect the environment to an extent that increases with the magnitude of flow changes. In order to address this issue, aquatic science needs to move to pilot or manipulation experiments (Bunn & Arthington, 2002). Without considering the mechanical abrasion, it is not possible to understand the global dynamics of organic matter detritus or measure the relative importance of any agent decomposer (Heard et al., 1999). Therefore, it is important to assess the influence of changes in water flow rate with experiments under controlled conditions so that the effects of change in the flow are not overlooked or underestimated.

In this study, we simulate the changes in water flow for the tributaries upstream and downstream of artificial reservoirs. More specifically, we test the hypothesis that an increase in the velocity of water flow causes increased physical fragmentation of the debris adduced from adjacent terrestrial vegetation. We assess the influence of the water flow velocity on the aerobic decomposition of leaves and twigs into the flumes, with controlled current velocities.

Materials and methods

Sampling of vegetation and soil

Sampling of plant resources were taken from three areas in the Atlantic Rain Forest, Rio de Janeiro State, Brazil (22° 19′S and 42° 41′W). The samples of leaves and twigs (diameter ≤1.0 cm) comprised mainly the

following taxa: *Schinus terebinthifolius*, *Cariniana estrellensis*, *Senna multijuga*, *Ormosia friburguesis*, *Alchornea* sp., *Croton* sp., *Inga* sp., *Trichilia* sp., Solanaceae. The set of leaves of different taxa were mixed, forming a mixed sample of leaves, and the set of twigs of the same taxa was mixed to compose the sample of twigs. Afterward, in the laboratory, the samples were dried (45°C) until they reached constant weight. Samples of surface soil (up to 5-cm depth) were also collected for preparation of incubation inocula. The soil samples were maintained at 10°C until the start of experiments.

Mass loss experiments

To evaluate the effects of current velocity on the aerobic degradation of leaves and stems (weight loss), two glass flumes were used. The first has 3.0-m internal length, 0.32 m of height and width, and 0.10 m^2 cross-sectional area. The water flow was generated by a centrifugal pump (Dancor, CHS 1 1/2 HP). The velocity of water flow was controlled by a frequency inverter (WEG, CFW080070T2024PSZ), which was monitored by a flowmeter (Contech, SVTL 50/50 2″). The monitoring of current velocity and the data acquisition were performed every 15 min with a control module (Compact Field Point; CFP) with a computer interface (LabVIEW software; National Instruments). The second flume was similar, with the difference of its length (4.50 m), and its velocity control was performed by a physical barrier. The smaller flume was used in the experiment with twigs, while the other was used for the decay of leaves. Despite the differences in size and in the flow control method, the results are comparable as the cross sections of the two flumes were the same and the velocities were kept constant along the flumes.

For each experiment, samples of leaves (4.0 g) and twigs (6.0 g) were placed within nylon litter bags (leaves: 10 × 15 cm; mesh size: 1 mm^2; twigs: 5 × 15 cm, mesh size of 1 mm^2). The differences in masses of leaves and twigs and in the dimensions of the litter bags were due to the greater volume occupied by the leaves. Each litter bag was pierced by a stainless steel rod in the longitudinal direction. The rods were used to fasten the litter bags in PVC supports obliquely crossed on the top of the flumes. At the bottom of the steel rod, the silicone suckers were placed for fixation of the litter bags on the flume bottom. In each PVC

support, five litter bags were placed, side by side. In the largest flume, 55 litter bags with leaves were placed. After perpendicular fixation of litter bags, 172 L of previously prepared inoculated medium were added; this volume was used to achieve 18 cm of water column height, thus guaranteeing that the litter bags were submersed with a water flow without cavitations in the suction end of the pump. The final ratio of leaves was 3.0 g L^{-1}. Likewise, in the smaller flume, 55 litter bags with twigs and 259 L of inocula (previously prepared) were placed. Again, this volume was used to achieve 18 cm of water column height; the final ratio of twigs was 3.0 g L^{-1}. Inocula were prepared by adding 1.0 kg of soil in 5.0-L of deionized water; after 6 h of incubation (at room temperature), the mixture was filtered (paper filter), with the final volumes being obtained (i.e., 172 and 259 L).

The leaves and twigs were incubated at three flow velocities: 0, 5, and 10 cm s^{-1}. For the velocity 0 cm s^{-1}, experiments were performed in two poly-ethylene carboys (vol.: 60 L) with 55 L inoculated medium and 33 litter bags with (5.0 g) of leaves or twigs, maintaining the proportion adopted in the flumes experiments (3.0 g L^{-1}). During the experiment, the carboys were kept under aeration to avoid anaerobic processes. Over a period of 4 months, 11 samples were taken for each experiment, corresponding to the days 1, 3, 5, 10, 15, 20, 30, 45, 60, 90, and 120. On every sampling day, five litter bags were taken from each flume, and three replicates from each carboy. The samples were dried (45°C) until it reached constant weight. On the sampling days, the electrical conductivity (conductivity meter Quimis, model Q 795P), pH (potentiometer Quimis, model Q 400BC), and the concentration of dissolved oxygen (oximeter YSI, model 55-12) were measured. The water temperature was maintained at 24.0 ± 1.0°C, with monitoring being performed every 15 min using a thermocouple immersed in water, and data acquisition with a CFP module.

Mathematical modeling and data analysis

The mass losses (average values) of the leaves and twigs detritus were fitted to a first-order kinetics model (Eq. 1; Bianchini & Cunha-Santino, 2011). The iterative Levenberg–Marquardt algorithm was used for parameterization of the model (Press et al., 2007), using no linear regressions.

$$POM = LSPOM \times e^{-k_T t} + RPOM \times e^{-k_R t} \qquad (1)$$

where POM is the particulate organic matter (%); LSPOM is labile and/or soluble fractions of the detritus (%); RPOM is refractory particulate organic matter (%); e is natural logarithm base (ca. 2.72); t is the time (days); k_T is the total rate constant of LSPOM loss (e.g., dissolution and oxidation of labile compounds), (days^{-1}); and k_R is the RPOM mass loss (e.g., chemical and microbial oxidation (mineralization) and abrasion) rate constant (days^{-1}).

The temporal variations of the detritus mass loss under different current velocities were statistically compared using a parametric test (ANOVA-Repeated Measures). When statistical differences were observed, the Tukey test, with significance level of 0.05, was performed to identify the differences among the groups. The software used in the statistical analyses was PAST, version 2.16 (Hammer et al., 2001).

Results

The mass losses of leaves and twigs for three current velocities were fitted to the double exponential decay model (Eq. 1), with determination coefficient $r^2 \geq$ 0.96, as shown in Table 1. Weight losses of the two types of detritus increased with increasing flow velocity (Fig. 1A, B; Table 1). The mass losses for leaves at velocities 5 and 10 cm s^{-1} were significantly higher ($P < 0.001$) than those in stagnated water, with significant difference ($P < 0.05$) observed in leaves decomposition under water flow velocities of 5 and 10 cm s^{-1}. Weight losses of twigs under 5 and

10 cm s^{-1} were significantly higher ($P < 0.001$) than those in stagnated water. There were no significant differences ($P = 0.33$) in the twigs' mass losses under 5 and 10 cm s^{-1} flow velocities. The mass loss was significantly higher ($P < 0.01$) for the leaves, except the mass losses of leaves at stagnated water and twigs under 10 cm s^{-1} ($P = 0.52$).

The difference in the mass losses of the detritus types increased with the current flow. The final masses of remaining material in stagnated water were higher (leaves 59.3% and twigs 81.2%). For the 5 cm s^{-1} velocity, the remaining mass of leaves was 50.9%, while for the twigs, it was 78.4%. For 10 cm s^{-1}, the remaining mass was 42.1% for the leaves and 74.7% for the twigs, i.e., a difference of 32.6% (Fig. 1). From the modeling with the kinetics parameters, we inferred that an increasing flow velocity tended to increase LSPOM and k_R, while decreasing RPOM and k_T for the decomposition of leaves and twigs (Table 1). Except for k_R (RPOM mass loss rate constant) for decomposition of leaves, which did not present a clear tendency in relation to flow velocity, the changes in the kinetic parameters exhibited a linear relationship with increasing current velocity (Table 1).

The electrical conductivity of water increased during decomposition of leaves and twigs, tending to stabilize after the 10th day (Fig. 1C, D). For decomposition of leaves, the electrical conductivity was significantly higher ($P < 0.01$) for the velocities of 5 and 10 cm s^{-1}. Conductivity was significantly higher ($P < 0.05$) for the leaves in all experimental conditions, except for the leaves in stagnated water and twigs, in respect of velocity at 10 cm s^{-1}, which presented statically the same values. The pH ranged between 5.5 and 8.3 in the leaves decomposition and between 4.7 and 7.8 for incubations with twigs (Fig. 1E, F). There were no significant differences ($P > 0.05$) in pH for decompositions of leaves and twigs in the three current velocities. The experiments always remained aerobic; in leaves decomposition (the more "labile" resource), dissolved oxygen concentrations varied between 2.73 and 8.09 mg L^{-1} at 0 cm s^{-1} (stagnated water), 3.71 and 8.27 mg L^{-1} at 5 cm s^{-1} and from 5.48 to 8.32 mg L^{-1} for 10 cm s^{-1}.

Table 1 Kinetic model parameterization (Eq. 1) for different current velocities (0, 5, and 10 cm s^{-1})

Resource	LSPOM (%)	RPOM (%)	k_T (days^{-1})	k_R (days^{-1})	r^2
Leaves					
0 cm s^{-1}	12.48	87.4	1.07	0.0033	0.99
5 cm s^{-1}	24.81	74.5	0.62	0.0036	0.99
10 cm s^{-1}	34.34	61.7	0.23	0.0033	0.98
Twigs					
0 cm s^{-1}	10.80	89.1	1.11	0.0008	0.98
5 cm s^{-1}	10.94	87.6	0.25	0.0010	0.96
10 cm s^{-1}	14.15	85.6	0.89	0.0012	0.98

Discussion

The coarse particulate organic matter (CPOM), including leaves and twigs, in lotic systems, is

modified according to one of the following three processes: (i) conversion into dissolved organic matter (DOM) via leaching; (ii) conversion into fine particulate organic material (FPOM) through organic decomposition or physical abrasion; and (iii) incorporation into the biomass of heterotrophic organisms or mineralization (Wallace et al., 1995). Most of the adduced CPOM is converted into FPOM and DOM, which are likely to be transported by the flows of water (Cuffney et al., 1990). In our study, the flow velocity caused the increase in mass losses for leaves and twigs detritus, suggesting an increase in the transports of FPOM and DOM. The effects from abrasion on decomposition of detritus (i.e., changes in reactions rates constants and chemical characteristics) also have been focused. In relation to the mineralization, the flow velocity improved the losses of mass of refractory material, mainly for twigs. The organic matter decomposition in streams has been usually attributed to the action of biotic agents (e.g., macroinvertebrates, fungi, etc.), without taking into account variations in water flow (Cummins et al., 1989; Graça & Canhoto, 2006). In addition, many studies which aimed at investigating flow changes in rivers and streams evaluated the influence on habitat and biotic composition diversity (e.g., fishes, macroinvertebrates, aquatic macrophytes, etc.), but not on the decomposition (Bunn & Arthington, 2002; Poff & Zimmerman, 2010).

The water flow characteristics of a given river or stream vary over a wide range of time and space. The velocity has a spatial variation at very small (4–10 m) and very large scales (102 m) of length. The temporal variations in current velocities occur at scales as small as those associated with the smaller eddies (ca. 2–10 s) to scales as large as the intervals of floods recurrence (ca. 10^7 s) (Hart & Finelli, 1999). In this study, it was possible to evaluate the effect of increasing flow velocity because in the flume, all samples were submitted, to the same velocity at all places over time. Even for small increments of current flow (0–5 cm s^{-1} and from 5 to 10 cm s^{-1}), differences in the detritus decomposition were already observed.

In this laboratory study, the increase in mass loss owing to abrasion suggests that, in lotic system, the changes in water flow and consequent physical fragmentation of the debris should have important ecological implications for their structure and functioning. Degradation provides materials and energy for these ecosystems communities (Wallace et al., 1997). The fast decomposition for the leaves—and not for twigs—is a recurrent pattern with the prevalence of labile organic matter decay in relation to the refractory material (Mathuriau & Chauvet, 2002; Allan & Castillo, 2007). The increase in flow velocity contributes to stressing the fiber (i.e., an increase of LSPOM values) and thereby converting the fractions of the refractory part of the detritus in a more labile and/or soluble material; and such conversions lead to increased mass loss as a whole. Decomposition studies (Cunha-Santino et al., 2010; Bianchini & Cunha-Santino, 2011; Silva et al., 2011; Tonin & Hepp, 2011) using the biphasic model of mass loss assumes that the proportions between LSPOM and RPOM depend mainly on the chemical composition of the resource. They usually do not consider the possibility of chemical alteration of the resource because of an external driving force. The reduction of k_T owing to an increased current flow also suggests the inclusion of more refractory material to the category of compounds that can be leached. Considering that RPOM is quantitatively the major fraction of detritus, and their mass loss is usually driven by slow biological processes (i.e., mineralization), the change of RPOM into LSPOM interferes with the energy flow yields of detritus chain. Thus, the material transferences that support the decomposer organisms into the sediments will sustain other trophic pathways. Small changes in k_R in the leaves decomposition suggest that the flow velocity tends not to increase the mass loss of more flexible resources. On the other hand, the action of abrasion (i.e., linear increase of k_R as a function of the flow velocity) in more rigid resources, such as the twigs, is clear.

With increasing current velocity, the leaves decomposition was more susceptible than that of the twigs (Fig. 1; Table 1), which is consistent with the greater fragility of this plant structure (Allan & Castillo, 2007). In addition, stronger abrasion effects should be expected owing to the larger surface area/volume ratios for the leaves. Therefore, leaf litter is an important supplier of FPOM and DOM for heterotrophic organisms. By increasing the flow velocity to 10 cm s^{-1}, the twigs also suffered abrasion effects. The consequent release of FPOM and DOM from the twigs debris, even on smaller quantities than in leaf litter, increases FPOM and DOM in the aquatic ecosystem, because the woody biomass in forests is
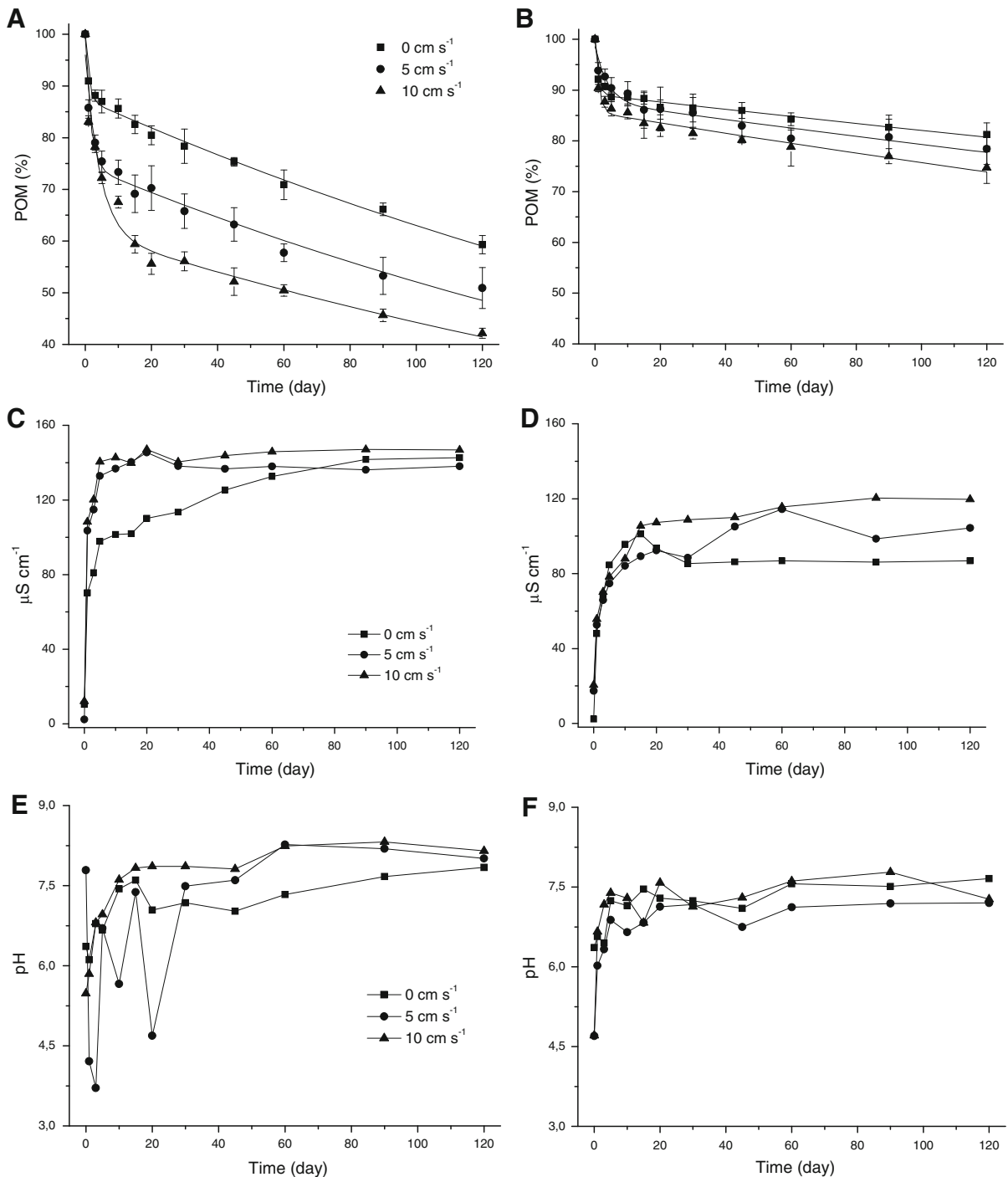
Fig. 1 The decomposition kinetics of leaves (**A**) and twigs (**B**) at three current velocities (0, 5, and 10 cm s^{-1}). Temporal variations of electrical conductivity during decomposition of leaves **C** and twigs (**D**). pH change during decomposition of leaves (**E**) and twigs (**F**) for distinct velocities (0, 5, and 10 cm s^{-1})

much greater than that of leaves (Delitti & Burger, 2000; Smithwick et al., 2002; Hart et al., 2003). The effects of a large increase in flow velocity on the physical fragmentation of twigs should be important in pulse discharge in lotic systems owing to seasonal variations between wet season and drought. The physical fragmentation occurs mainly in ecosystems with natural flow, as in rivers having dams, there is a flow homogenization, with low magnitude and shorter duration of variation (Lytle & Poff, 2004; Poff et al., 2007). In the case of homogeneous flows, the effects from the current on the fibers stress (i.e., lignocellulosic matrix) of detritus should be predominant (as seen in k_T and LSPOM values).

Different relationships between changes in flow velocity and physical fragmentation of debris have been reported in the literature. In a similar study with leaves, no significant differences were found in decomposition under current velocities of 5 and 20 cm s^{-1} (Ferreira et al., 2006), and they attributed the results to the small change in velocities tested. The discrepancies between the two studies may be caused by other variables, such as chemical composition and structural aspects (e.g., toughness) of detritus.

Field studies have attributed changes in the decomposition of plant resources owing to the streams' and rivers' flow velocities (e.g., Rueda-Delgado et al., 2006; Niu & Dudgeon, 2011); nevertheless, not always the temporal and spatial variations in flow velocity allow for precise conclusions to be drawn about their influence (Hoover et al., 2006). Furthermore, differences in decomposition rates between species were observed, thus showing that the chemical composition of detritus was also an important factor. Mechanical fragmentation was shown to be important in the detritus mass loss, but other factors (e.g., light, temperature) could have synergistic influence (Carvalho & Ueda, 2009). Decomposing microorganisms were proven more important in the leaves decomposition in streams than the current velocity or invertebrate shredders (Rader et al., 1994; Imberger et al., 2008).

The present study supported the hypothesis that the increase in current velocity promoted physical fragmentation of plant detritus. k_T values actually decrease with increasing flow velocity (except for 5–10 cm s^{-1}). LSPOM content increased with increasing flow velocities, probably because of the physical stress and abrasion, especially in the leaves decomposition. Thus,

compounds that would exhibit refractory properties in stagnated water became leachable owing to abrasion by the action of water. This effect may have consequences during the formation of a reservoir. When newly flooded, the terrestrial vegetation situated in the upstream region (riverine zone; sensu Kimmel et al., 1990) will be more rapidly degraded than that located nearer to the dam (i.e., lacustrine zone with prevalence of lentic characteristics). Furthermore, it is also necessary to consider that the current velocity varies spatially as a function of depth, being lower near the sediment and, crossways, and even lower in the edges. The positioning of the detritus may determine the current velocity (i.e., increase in the roughness coefficient) as well, thus affecting the half-time of detritus decomposition (Menéndez et al., 2012). The flow velocity also depends on the river's order and on hydrological events (rain), affecting the abrasion of water over the detritus. Nevertheless, according to the experimental conditions adopted, we could conclude that the flow velocity presented similar effects in the leaves and twigs decomposition. The raise of flow velocity tends to change the refractory fractions (i.e., lignocellulosic matrix) into more labile/soluble compounds and increase the values of RPOM rate constant, owing to the mechanical abrasion. It is also possible that the flow causes stress to the fibers and increases the leaching from compounds that would be otherwise not easily leached. To clarify these questions, we suggest that the detritus fibers are subjected to microscopy studies and tests with specific resistance assays.

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