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The fate of C<sub>4</sub> and C<sub>3</sub> macrophyte carbon in central Amazon floodplain waters: insights from a batch experiment

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## 1 **Summary**

2 The central Amazon floodplains are particularly productive ecosystems, where a large  
3 diversity of organic carbon sources are available for aquatic organisms. Despite the fact that  
4 C<sub>4</sub> macrophytes generally produce larger biomasses than C<sub>3</sub> macrophytes, food webs in the  
5 central Amazon floodplains appear dominantly based on a C<sub>3</sub> carbon source.

6 In order to investigate the respective fate and degradation patterns of C<sub>4</sub> and C<sub>3</sub> aquatic plant-  
7 derived material in central Amazon floodplains, we developed a 23-days batch experiment.

8 Fatty acid and carbon concentrations as well as stable isotope compositions were monitored  
9 over time in 60 L tanks. These tanks contained Amazon water, with different biomasses of C<sub>3</sub>  
10 and C<sub>4</sub> macrophyte, representative of *in situ* densities occurring in central Amazon  
11 floodplains.

12 In the C<sub>4</sub> *Paspalum repens* treatments, organic (POC, DOC) and inorganic carbon (DIC) got  
13 rapidly enriched in <sup>13</sup>C, whereas in the C<sub>3</sub> *Salvinia auriculata* treatments, POC and DOC  
14 showed little change in concentration and isotopic composition, and DIC got depleted in <sup>13</sup>C.  
15 The contribution of *P. repens* to POC and DOC was estimated to reach up to 94.2 and 70.7 %,  
16 respectively. In contrast, no differences were reported between the C<sub>3</sub> *S. auriculata* and  
17 control treatments, an observation attributed to the lower C<sub>3</sub> biomass encountered in the field,  
18 to a slower degradation rate of C<sub>3</sub> compared to C<sub>4</sub> compounds, and to similar isotopic  
19 compositions for river POC and DOC, and C<sub>3</sub> compounds.

20 The <sup>13</sup>C enrichments of POC, DOC, and DIC from *P. repens* treatments were attributed to an  
21 enhanced bacterially-mediated hydrolysis and mineralization of C<sub>4</sub> material. Evolutions of  
22 bacterial abundance and branched fatty acid concentrations confirmed the role of  
23 heterotrophic microbial communities in the high *P. repens* decomposition rate. Our  
24 experiment highlights the predominant role of C<sub>4</sub> aquatic plants, as a large source of almost  
25 entirely biodegradable organic matter available for heterotrophic activity and CO<sub>2</sub> outgassing  
26 to the atmosphere.

27

27

28 **Introduction**

29 One of the largest sources of organic carbon in Amazon floodplains is derived from aquatic  
30 macrophytes, which contribute up to half of the ecosystem primary production (Melack &  
31 Forsberg, 2001). These macrophytes grow emerged, submerged or floating, with 388 species  
32 described in a várzea (i.e. white-water nutrient rich floodplain) located near the city of  
33 Manaus, in central Amazon (Junk & Piedade, 1993b). Among the most abundant species, the  
34 floating grasses *Echinochloa polystachya* and *Paspalum fasciculatum* (Poaceae family) can  
35 reach biomasses of 80 and 60 t ha<sup>-1</sup>, respectively (Junk & Piedade, 1993a; Piedade et al.,  
36 1991). Another macrophyte largely represented in the várzea is *P. repens* (up to 22 t ha<sup>-1</sup>,  
37 Fig. 1, Junk & Piedade, 1993a). These aerial species, which convert atmospheric carbon  
38 dioxide into biomass through a C<sub>4</sub> pathway, constitute floating meadows that can extend over  
39 large areas of floodplains (Junk & Howard-Williams, 1984; Hess et al., 2003; Silva et al.,  
40 2013). Amazon floating meadows may also be composed of macrophytes using the C<sub>3</sub>  
41 photosynthetic pathway such as *Eichhornia* sp., *Pistia stratiotes* and *Salvinia auriculata*  
42 (Fig. 1). However, the biomass of all these C<sub>3</sub> macrophytes add up to 3 to 15 t ha<sup>-1</sup> only  
43 (Furch & Junk, 1992).

44 The ecology of C<sub>3</sub> and C<sub>4</sub> macrophytes, and particularly their biomass and production rates,  
45 have been thoroughly examined (e.g. Morison et al., 2000; Engle et al., 2008; Silva et al.,  
46 2013). Despite their large abundance, C<sub>4</sub> macrophytes constitute a minor source of energy for  
47 Amazon aquatic food webs (Hamilton et al., 1992; Forsberg et al., 1993; Mortillaro et al.,  
48 2015) and modest contributors to particulate organic carbon (POC, Hedges et al., 1986;  
49 Mortillaro et al., 2011; Moreira-Turcq et al., 2013). Indeed, C<sub>4</sub> macrophytes are largely <sup>13</sup>C  
50 enriched (-12 ‰, Hedges et al., 1986; Mortillaro et al., 2011) compared to POC in rivers and  
51 várzea of the Amazon (-30 ‰, Quay et al., 1992; Hedges et al., 1994). The almost constant  
52 isotopic composition of dissolved organic carbon (DOC), at around -29 ‰ in the Amazon  
53 River, suggests a dominant C<sub>3</sub> source such as terrestrial plants and/or macrophytes. In  
54 contrast, dissolved inorganic carbon (DIC) is much heavier (-17.7 to -11.5 ‰, Quay et al.,  
55 1992), i.e. closer to C<sub>4</sub> macrophytes signature, but also closer to the signature of atmospheric  
56 CO<sub>2</sub>. This isotopic composition results from isotopic equilibration induced by CO<sub>2</sub> gas  
57 exchange (Quay et al., 1992; Hedges et al., 1994; Mayorga et al., 2005; Abril et al., 2014),  
58 and/or due to carbonate mineral weathering (e.g. chemical or mechanical decay of rocks,  
59 Mayorga et al., 2005).

60 Previous macrophyte (C<sub>3</sub> and C<sub>4</sub>) degradation experiments in litterbags, exposed to natural  
61 weathering, found an initially rapid loss of weight and a decrease in nutrients  
62 (Howard-Williams & Junk, 1976; Furch & Junk, 1992). However, the contribution of  
63 macrophytes to the Amazon aquatic food webs was not verified by Fellerhoff et al. (2003) in  
64 their degradation experiment. Therefore, in order to examine the apparent discrepancy  
65 between the high biomass of C<sub>4</sub> macrophytes in the floodplains and their modest contribution  
66 to the organic matter (OM) pool in the Amazon river-floodplain ecosystem, a degradation  
67 experiment was designed to investigate the fate of carbon from C<sub>4</sub> and C<sub>3</sub> macrophytes in  
68 microcosms. Particulate and dissolved carbon concentrations, stable isotope compositions and  
69 fatty acids (FA) concentrations, were analyzed in large volumes of Amazon waters incubated  
70 with variable amounts of a C<sub>4</sub> and a C<sub>3</sub> macrophyte. Bacterial abundance and nutrient  
71 concentrations complemented the description of macrophyte degradation throughout a 23-day  
72 experiment. Our work hypothesis was that very fast decomposition and mineralization of C<sub>4</sub>  
73 macrophytes explain their low contribution to central Amazon aquatic food webs.

74

## 75 **Material and methods**

### 76 *Sampling*

77 In order to follow the fate of OM during the degradation of two aquatic macrophytes and the  
78 influence of degradation products on the quality of POM, samples of *P. repens* (C<sub>4</sub>) and  
79 *S. auriculata* (C<sub>3</sub>, Fig. 1) were collected in the Camaleão Lake (várzea), located by the  
80 Solimões River. These two macrophytes were selected for their widespread distribution in  
81 central Amazon floodplains and their large FA concentration compared to other macrophyte  
82 species (i.e. *Eichhornia* sp. and *Pistia stratiotes*), as characterized in a previous study  
83 (Mortillaro et al., 2011).

84 Macrophyte samples were sorted in order to eliminate dead leaves and washed to remove  
85 sediment and invertebrates. About 900 L of water were also sampled from the lake and  
86 distributed into 15 microcosms of 60 L each. Three water samples and three portions of each  
87 macrophyte were collected in order to get their initial composition (i.e. stable isotopes and  
88 FA).

### 89 *Experimental setup*

90 The experiment was implemented on the *Yane José IV* boat in August-September 2010. Five  
91 experimental treatments were used: high and low biomasses of *P. repens* (PR-HB and PR-LB,  
92 respectively) and *S. auriculata* (SA-HB and SA-LB, respectively), as well as a control

93 without macrophyte (Ctrl). These five treatments were selected to distinguish species effect  
94 from biomass effect on water characterization. For each treatment, triplicate microcosms were  
95 used. In PR-HB microcosms, 250 g of fresh *P. repens* leaves (25.6 gC) were used. This  
96 amount was estimated from a maximum dry biomass of 22 t ha<sup>-1</sup> (recorded in the Januári  
97 Lake near Camaleão Lake, Junk & Piedade, 1993a), with less than one fifth of emerged  
98 *P. repens* biomass (Silva et al., 2009), an estimated water proportion of 75.9 % and a  
99 microcosms surface of 0.13 m<sup>2</sup>. Similarly, the mean *S. auriculata* dry biomass was estimated  
100 to be 1 t ha<sup>-1</sup> (Junk & Piedade, 1997) giving a theoretical wet weight of 200 g (93.5 % of  
101 water). However, low biomasses of *S. auriculata* were available during sampling, so that only  
102 100 g (2.3 gC) per microcosm were used (SA-HB). Low biomass treatments contained 10 %  
103 of the high biomass amount for each species (25 g of macrophytes for PR-LB and 10 g for  
104 SA-LB). Macrophyte leaves were introduced into microcosms filled with floodplain water,  
105 and were kept in the dark under constant temperature conditions (28 °C). Permanent stirring  
106 with a water pump ensured oxygenation of the microcosms (from 40 to 100 % air-saturation)  
107 and avoided anaerobic conditions to occur. Although low dissolved oxygen is common under  
108 floating macrophytes in várzea (~50 % saturation, Engle & Melack, 1993), permanent  
109 oxygenation was maintained in order to match natural conditions within floating meadows in  
110 open waters, where wind and water currents are sufficient to maintain aerated to hypoxic  
111 waters (30 % min) in 2-6 meter depth water column (Vidal et al., 2015).  
112 In each treatment, samples were collected after 3, 6, 12, 18 and 23 days of experiment. At  
113 each sampling time, around 3.5 L of water were collected and pre-filtered on 200 µm to avoid  
114 heterogeneity between samples due to contamination with macrophyte fragments.  
115 Consequently, POC concentrations reported here concern the fraction smaller than 200 µm.  
116 Microcosms volume (60 L) was chosen so that at the end of the experiment, 70 % of the  
117 initial water volume was still available, to avoid any concentration bias in the course of the  
118 experiment.

### 119 *Sample analyses*

120 The FA compositions of POM and macrophytes were analyzed with a gas chromatograph  
121 (Varian CP-3800 with flame ionization detector) after extraction, following a modified  
122 method of Bligh & Dyer (1959) as described in Mortillaro et al. (2011). POM samples were  
123 obtained after immediate on-board filtration (GF/F, 0.7 µm, pre-combusted 12 h at 450 °C)  
124 using a vacuum system under low pressure, after which filters were freeze dried and stored at  
125 -20 °C until analysis. The carbon and nitrogen compositions, and isotopic ratio (<sup>13</sup>C/<sup>12</sup>C or  
126 <sup>15</sup>N/<sup>14</sup>N), of dried POM and macrophyte samples were determined at the UC Davis Stable

127 Isotope Facility and reported in standard delta notation ( $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$ ), defined as parts per  
128 thousand (‰) deviation from a standard (Vienna PeeDee Belemnite for  $\delta^{13}\text{C}$  and atmospheric  
129  $\text{N}_2$  for  $\delta^{15}\text{N}$ , Peterson & Fry, 1987). The DOC concentrations and isotopic compositions  
130 ( $\delta^{13}\text{C}$ -DOC) were determined using an EA-IRMS analyzer following the protocol of Alberic  
131 (2011). The DIC isotopic compositions ( $\delta^{13}\text{C}$ -DIC) were also determined using an EA-IRMS  
132 analyzer following the protocol of Bouillon et al. (2007). However, DIC concentrations were  
133 not measured, as microcosms were continuously aerated with pumps. The concentration of  
134 nitrites ( $\text{NO}_2^-$ ), nitrates ( $\text{NO}_3^-$ ) and ammonium ( $\text{NH}_4^+$ ) dissolved fractions, summarized as  
135 DIN (dissolved inorganic nitrogen), as well as orthophosphate concentrations ( $\text{PO}_4^{3-}$ ) were  
136 determined by spectrophotometry following a modified method of Grasshoff (1999). Total  
137 bacterial abundances were determined by direct epifluorescence microscopy counting, using  
138 4,6-diamidino-2-phenyl-indole (DAPI) up to a final concentration of  $1 \mu\text{g mL}^{-1}$  after 15 min  
139 of incubation (Porter & Feig, 1980). Direct counts were performed at 1 250x magnification,  
140 under an epifluorescence microscope (Leica Leitz DMR; 365 nm). In turbid samples (high  
141 suspended matter content), subsamples were pre-treated (before staining) by addition of  
142 150  $\mu\text{l}$  of Tween, sonicated at 35 khz for 5 min, and centrifuged at 3 000 g during 10 min at  
143  $4^\circ\text{C}$  (Chevaldonne & Godfroy, 1997; Hubas et al., 2007a, 2007b).

#### 144 *Data analysis*

145 The data obtained for each microcosm were compared, to evidence variations between  
146 treatments. All FA of POM (up to 40) were used in these analyzes without transformation and  
147 were represented by their relative proportions. A dissimilarity matrix between each pair of  
148 samples was calculated using the Bray-Curtis index. Dissimilarities between samples were  
149 then graphically represented using an nMDS (non-metric MultiDimensional Scaling, Zuur et  
150 al., 2007). Differences between groups were tested using analyzes of similarities tests  
151 (ANOSIM, Oksanen et al., 2010), without considering temporal variability. When differences  
152 were significant, a similarity percentages analysis (SIMPER, Oksanen et al., 2010) was used  
153 to determine the relative contribution of each FA to differences between two groups.  
154 The differences in the isotopic compositions ( $\delta^{13}\text{C}$ -DOC,  $\delta^{13}\text{C}$ -POC,  $\delta^{15}\text{N}$ -PON and  
155  $\delta^{13}\text{C}$ -DIC) as well as differences in POC, DOC, DIN,  $\text{PO}_4^{3-}$  concentrations and bacterial  
156 abundance between treatments ( $n = 5$ ) were tested using a non-parametric Kruskal-Wallis test  
157 (KW). Non-parametric Mann-Whitney-Wilcoxon (MWW) Post-Hoc tests were then used to  
158 identify the differences between individual treatments, after correction following a Benjamini  
159 and Hochberg (BH) procedure for multiple comparisons (Benjamini & Hochberg, 1995).



160 The relative contribution of  $C_4$  macrophytes to POM was calculated using a two end member  
 161 mixing model (Forsberg et al., 1993):

$$162 \quad \%C_4 = \left[ 1 - \frac{\delta^{13}C_{source} - \delta^{13}C_{C_4}}{\delta^{13}C_{T_0} - \delta^{13}C_{C_4}} \right] \times 100 \quad (\text{Eq. 1})$$

163 where  $\delta^{13}C_{source}$  was the  $\delta^{13}C$ -POC compositions for each time and treatment,  $\delta^{13}C_{C_4}$  was the  
 164 mean *P. repens* composition,  $\delta^{13}C_{T_0}$  was the mean POM composition at the beginning of the  
 165 experiment and %  $C_4$  the *P. repens* contribution to the isotopic compositions of OM in each  
 166 sample.

167 All statistical analyzes were implemented within the R programming environment (R  
 168 Development Core Team 2010, package Vegan, Oksanen et al., 2010), with the probability  $\alpha$   
 169 set at 0.05.

170

## 171 Results

172 Among macrophyte samples, 41 FA were identified (Table 1) with an intragroup similarity of  
 173 92.5 and 93.2 % within *P. repens* and *S. auriculata*, respectively, at the beginning of the  
 174 experiment. *P. repens* was  $^{13}C$  and  $^{15}N$  enriched compared to *S. auriculata* (Table 1).

175 The water collected in the várzea was characterized by 37 FA (Table 1), where saturated 14:0,  
 176 15:0, 16:0 and 18:0 accounted for 70 % of the total FA composition of POM. The POC and  
 177 DOC concentrations were respectively of  $1.3 \pm 0.1$  and  $2.8 \pm 0.3$  mg L<sup>-1</sup> (Fig. 3), with a  
 178 carbon isotopic composition of  $-30.1 \pm 0.4$  ‰ for POC and  $-28.7 \pm 0.4$  ‰ for DOC (Fig. 4).  
 179 DIC was  $^{13}C$  enriched relative to POC and DOC ( $\delta^{13}C$ -DIC of  $-11.9 \pm 0.2$  ‰, Fig. 4).

180 Water from the five treatments showed significant differences in their global FA compositions  
 181 (ANOSIM,  $R = 0.35$ ,  $p < 0.001$ , Fig. 2). Samples from Ctrl, SA-LB, SA-HB, and PR-LB had  
 182 a similar FA composition but differed from samples of PR-HB (Table 2). Similarities in the  
 183 FA composition within each treatment were higher than 77 % (Table 3). A higher proportion  
 184 of branched FA (mainly 15:0iso and 15:0anteiso) and a lower proportion of 18:0 were  
 185 observed in PR-HB compared to other treatments (Table 3). The concentrations of POC,  
 186 DOC, DIN,  $PO_4^{3-}$  as well as  $\delta^{13}C$ -POC,  $\delta^{13}C$ -DOC,  $\delta^{13}C$ -DIC and bacterial abundance  
 187 displayed significant differences between treatments (KW,  $p < 0.001$ , Table 4, Figs. 3-5),  
 188 whereas  $\delta^{15}N$ -PON was similar between all treatments (KW,  $p = 0.73$ ).

189 The highest concentrations of POC, DOC, DIN,  $PO_4^{3-}$  and highest bacterial abundance, were  
 190 observed in PR-HB (Figs. 3 & 5, Table 4). However, a higher POC concentration was

191 recorded in SA-HB compared to PR-LB and SA-LB (Table 4, Fig. 3). No differences in DOC  
192 concentration were observed between SA-HB, PR-LB and Ctrl, whereas SA-LB displayed the  
193 lowest DOC concentration. In contrast, the  $\delta^{13}\text{C}$ -POC was significantly higher in PR-HB  
194 ( $-14.3 \pm 1.0 \text{ ‰}$ ) and in PR-LB ( $-21.0 \pm 3.1 \text{ ‰}$ ) compared to other treatments (Fig. 4, Table 4).  
195 However, no difference was found between the isotopic compositions of SA and Ctrl  
196 treatments (MWW,  $p > 0.05$ , Table 4). The contribution of *P. repens* to the  $^{13}\text{C}$  enrichment  
197 recorded in POC from PR-HB and PR-LB reached 94.2 and 63.2 %, respectively (Fig. 4,  
198 Eq. 1). Similarly, the highest  $\delta^{13}\text{C}$ -DOC was recorded in PR-HB ( $-17.8 \pm 1.2 \text{ ‰}$ ) with a  
199 contribution of *P. repens* to the DOC of 70.7 % (Fig. 4, Eq. 1). A higher  $\delta^{13}\text{C}$ -DOC was also  
200 observed in PR-LB ( $-24.9 \pm 1.0 \text{ ‰}$ , Fig. 4, Table 4) compared to SA-HB and SA-LB, with a  
201 contribution of *P. repens* to the DOC reaching 27.8 %. A significant increase in  $\delta^{13}\text{C}$ -DIC was  
202 only recorded for PR-HB ( $-5.9 \pm 2.9 \text{ ‰}$ , Fig. 4, Table 4), concomitantly to a decrease in  
203  $\delta^{13}\text{C}$ -DIC for SA-HB ( $-17.8 \pm 3.7 \text{ ‰}$ , Fig. 4, Table 4). In contrast, no differences were found  
204 between the Ctrl with both SA and PR low biomass treatments (MWW,  $p > 0.05$ , Table 4).  
205  $\delta^{13}\text{C}$  of organic and inorganic matters increased after 3 to 6 days in PR treatments, whereas no  
206 temporal trends were recorded for Ctrl and SA treatments except for  $\delta^{13}\text{C}$ -DIC of SA-HB  
207 (Fig. 4).

208

## 209 Discussion

210 The present microcosm experiment highlights significantly different degradation patterns of  
211 two  $\text{C}_3$  and  $\text{C}_4$  Amazon macrophytes. Over a 23 day experiment, our results revealed a major  
212 impact of *P. repens* degradation, at high biomass, on OM composition. This impact was  
213 apparently related to the biomass of macrophytes used in the experiment as well as to the  
214 inherent biodegradability of  $\text{C}_4$  compared to  $\text{C}_3$  macrophytes. Indeed, even though the fast  
215 degradation of the  $\text{C}_4$  macrophyte was most evident in PR-HB, as revealed by all measured  
216 parameters, it was also observed in the PR-LB. For instance, PR-LB treatments (25 g of fresh  
217 macrophytes in a 60 L tank) showed stronger  $^{13}\text{C}$  enrichment in POC and DOC than SA-HB  
218 (100 g of macrophytes in a 60 L tank). There was however a slight increase in POC  
219 concentrations as well as a decrease in  $\delta^{13}\text{C}$ -DIC in the *S. auriculata* high biomass treatments  
220 that reveals on-going degradation.

221 In this experiment, *P. repens* displayed large proportions of 18:2 $\omega$ 6 and 18:3 $\omega$ 3  
222 polyunsaturated FA (up to 44 % of total FA), which is consistent with previous  
223 characterization of this FA as markers of macrophytes in this environment (Mortillaro et al.,

224 2011). Similarly, carbon stable isotope compositions of both *P. repens* and *S. auriculata* were  
225 consistent with those expected from plants with C<sub>4</sub> and C<sub>3</sub> photosynthetic pathways  
226 (-13.0 ± 0.8 and -30.5 ± 0.5 ‰, respectively, Smith & Epstein, 1971).

#### 227 *Contribution of P. repens (C<sub>4</sub>) and S. auriculata (C<sub>3</sub>) to POM*

228 In PR treatments, POC was significantly enriched in <sup>13</sup>C, which indicates a contribution of *P.*  
229 *repens*, after its hydrolysis into the POM pool. This contribution was estimated to reach 94.2  
230 and 63.2 % of total POM composition for PR-HB and PR-LB, respectively, using a two-end-  
231 member mixing model. This was surprising as previous studies, characterizing POM in the  
232 Amazon Basin, suggested a low contribution of C<sub>4</sub> macrophytes (Hedges et al., 1986;  
233 Mortillaro et al., 2011; Moreira-Turcq et al., 2013). The contribution of *P. repens* to POM  
234 was confirmed by the increased proportion of branched FA in PR treatments (15:0iso and  
235 15:0anteiso). These FA are regularly described as biomarkers of bacteria (Volkman et al.,  
236 1980; Kaneda, 1991; Mfilinge et al., 2003) and suggest here that in addition to hydrolysis,  
237 *P. repens* leaves were decomposed by heterotrophic microbial communities. Indeed, the  
238 transfer of FA to POM, including branched FA, was previously recorded from decomposing  
239 mangroves (Mfilinge et al., 2003). Similarly, the transfer of FA and the <sup>13</sup>C enrichment of  
240 POM and sediments were evidenced in salt-marsh from the decomposition of the C<sub>4</sub> *Spartina*  
241 spp. (Boschker et al., 1999). In salt-marsh ecosystems, the composition of POM affected by  
242 *Spartina* spp. decomposition changed from predominantly unsaturated to branched and  
243 saturated FA typical of bacteria (Johnson & Calder, 1973; Schultz & Quinn, 1973). Similar  
244 findings were reported in PR-HB and differences in FA compositions and <sup>13</sup>C enrichments  
245 reported for OM between PR and Ctrl treatments occurred in the first 3 to 6 days of the  
246 experiment. These changes in OM composition, as well as high bacterial abundance recorded  
247 in PR-HB, suggest a fast decomposition of this macrophyte, which may have exceeded  
248 hydrolysis (in agreement with previous studies; Fellerhoff et al., 2003).

249 Contrastingly to *P. repens*, no differences were reported between SA and Ctrl treatments for  
250 FA and δ<sup>13</sup>C-POC. Yet, decomposition of *S. auriculata* could not be excluded using  
251 δ<sup>13</sup>C-POC analyses. Indeed, fresh leaves of *S. auriculata* (-30.5 ± 0.5 ‰) had a similar  
252 composition to POM (-30.1 ± 0.4 ‰) at the beginning of the experiment. However, the higher  
253 POC concentrations measured in SA-HB compared to PR-LB and SA-LB suggest an effective  
254 hydrolysis of this macrophyte. The lack of differences between SA and Ctrl treatments for FA  
255 compositions and δ<sup>13</sup>C-POC suggest however a slower hydrolysis of *S. auriculata* compared  
256 to *P. repens*. Indeed, Howard-Williams & Junk (1976) recovered 50 % of *S. auriculata* initial  
257 dry weight at the end of a 186 days decomposition experiment. Similarly, Fellerhoff et al.

258 (2003) recovered 80 % of *S. auriculata* initial dry weight after 21 days of incubation. During  
259 our experiment, large macrophyte debris were observed for a much longer time in the  
260 *S. auriculata* treatments than in the *P. repens* treatments. This higher resistance to  
261 fractionation of the C<sub>3</sub> macrophyte was consistent with the differences in FA, POC and  
262  $\delta^{13}\text{C}$ -POC of the fine POM fraction (<200  $\mu\text{m}$ ).

### 263 *Impact of macrophyte degradation on dissolved compounds*

264 Decomposition of *P. repens* tissues led to a  $^{13}\text{C}$  enrichment of DOC and DIC. Such increase  
265 of  $\delta^{13}\text{C}$ -DIC resulted from bacterial mineralization of macrophyte organic carbon and CO<sub>2</sub>  
266 equilibration at the air/water interface (Quay et al., 1992; Hedges et al., 1994; Mayorga et al.,  
267 2005). Because the experiment was performed in contact with air in order to maintain aerobic  
268 conditions, the  $\delta^{13}\text{C}$ -DIC signature was affected by isotopic equilibration with the  
269 atmosphere. This process tends to slowly increase the  $\delta^{13}\text{C}$ -DIC to a value close to the  
270 isotopic equilibrium with the atmosphere at around 0 ‰ (Polsenaere & Abril, 2012).  
271 Consequently, the observed  $\delta^{13}\text{C}$ -DIC values are the result of a balance between the DIC  
272 production from the C<sub>3</sub> or C<sub>4</sub> plants decomposition and equilibration with the atmosphere. In  
273 SA-HB, the rapid  $\delta^{13}\text{C}$ -DIC decrease from  $-11.9 \pm 0.2$  ‰ at the beginning of the experiment  
274 to  $-20.3 \pm 7.0$  ‰ after 3 days of incubation reveals that the C<sub>3</sub> macrophytes were undergoing  
275 mineralization processes. Indeed, hydrolysis tends to leach out compounds relatively enriched  
276 in  $^{13}\text{C}$  with respect to more recalcitrant compounds (e.g. lignin) depleted in  $^{13}\text{C}$  (Costantini et  
277 al., 2014).

278 Previous works in the Amazon have attributed  $^{13}\text{C}$  enrichment of DIC to the preferential  
279 oxidation of organic carbon derived from C<sub>4</sub> macrophytes (Rai & Hill, 1984; Chanton et al.,  
280 1989; Quay et al., 1992; Waichman, 1996). Several other studies based on solute distribution  
281 suggested that C<sub>4</sub> grasses are more biodegradable than the bulk OM (Hedges et al., 1986;  
282 Quay et al., 1992; Mayorga et al., 2005). Ellis et al. (2012) have measured the  $\delta^{13}\text{C}$  of respired  
283 CO<sub>2</sub> in closed incubations at different stages of the hydrological cycle in the Solimões River  
284 and concluded that C<sub>3</sub> plants, C<sub>4</sub> plants and phytoplankton, all contributed to respiration in the  
285 Amazon River. The results of our incubations suggest however that high macrophyte  
286 biomasses are necessary in order to significantly alter the  $\delta^{13}\text{C}$ -DIC signature locally.  
287 Besides carbon, the nitrogen (N) and phosphorus (P) concentrations in floodplain waters were  
288 also affected by the decomposition and mineralization of macrophytes. A large release of PO<sub>4</sub>,  
289 DIN and potassium (K) was previously evidenced during the decomposition of  
290 *P. fasciculatum* (Furch & Junk, 1992). The decomposition of *P. fasciculatum* had the potential  
291 to supply floodplains with 242 kg ha<sup>-1</sup> of N and 66 kg ha<sup>-1</sup> of P in Furch & Junk (1992)

292 nutrients budget. Following these authors' calculations (i.e. maximum amounts of bio-  
293 elements released to water reported to maximum macrophyte biomasses), *P. repens* showed  
294 the potential, in our degradation experiment, to supply floodplains with 176.4 kg ha<sup>-1</sup> of N and  
295 48.2 kg ha<sup>-1</sup> of P. On the other hand, *S. auriculata* contribution to floodplains is estimated to  
296 reach 0.13 kg ha<sup>-1</sup> of N and 2.44 kg ha<sup>-1</sup> of P only. Therefore, our study demonstrates that  
297 *P. repens* represents a predominant source of N and P.

298 Fast nutrient recycling from decomposing macrophytes may fertilize Amazon floodplains,  
299 where N and P are growth-limiting factors (Devol et al., 1984; Forsberg, 1984; Setaro &  
300 Melack, 1984). Within the Amazon Basin, aquatic grasses such as *P. repens* have been  
301 suggested to be able of atmospheric N<sub>2</sub> fixation (Martinelli et al., 1992), so that atmospheric  
302 N<sub>2</sub> may contribute up to 90 % of plant N for stands of *P. repens* (Kern & Darwich, 2003).  
303 Therefore, the fast decomposition of N<sub>2</sub> fixing macrophytes may play a predominant role as a  
304 natural fertilizer for floodplains (Piedade et al., 1991; Kern & Darwich, 2003), stimulating  
305 phytoplankton production during the falling water period, when macrophytes start to  
306 decompose (Rai & Hill, 1984).

307 In Amazon floodplains, *P. repens* maximum biomasses were observed during the wet season  
308 (Junk & Piedade, 1993b, Silva et al., 2009), where C<sub>4</sub> macrophyte contribution to the primary  
309 production in várzea was estimated to reach 65 % (Melack & Forsberg, 2001). During this  
310 season, POC and DOC mainly originate from depleted carbon sources similar to C<sub>3</sub> primary  
311 producers (Hedges et al., 1994, Mortillaro et al., 2011). However during the dry season,  
312 macrophytes are subject to intensive degradation as water level decreases (Engle et al., 2008).  
313 An increasing contribution of macrophytes to OM composition, due to the accumulation of  
314 plant detritus, was suggested in the Amazon várzea (Mortillaro et al., 2011). However,  
315 although macrophytes have been demonstrated experimentally to affect the  $\delta^{13}\text{C}$ -POC and  
316  $\delta^{13}\text{C}$ -DOC, fast microbial mineralization of organic carbon suggests that only large  
317 macrophyte biomasses, produced during the flood season, have the potential to affect  
318  $\delta^{13}\text{C}$ -POC and  $\delta^{13}\text{C}$ -DOC within floodplains. Indeed, C<sub>4</sub> material may contribute to sediments  
319 OM composition (Sobrinho et al., 2016) according to spatial variability in C<sub>4</sub> macrophytes  
320 (Hess et al., 2003), despite a low burial of organic carbon in floodplain sediments (Moreira-  
321 Turcq et al., 2004). Therefore, most C<sub>4</sub> macrophytes are mineralized (Piedade et al., 1991;  
322 Junk & Piedade, 1993a) and thus contribute significantly to CO<sub>2</sub> outgassing, as previously  
323 suggested (Quay et al., 1992). Moreover, bacterial growth has been shown, within Amazon  
324 floodplains, to display a low efficiency (Vidal et al., 2015). This low efficiency implies,  
325 besides high respiration rates, a low transfer of C<sub>4</sub> carbon to higher trophic levels. The

326 production of C<sub>3</sub> macrophytes within the central Amazon Basin is much more limited than C<sub>4</sub>  
327 macrophytes (Furch & Junk, 1992). However, the lower lability of these macrophyte debris  
328 compared to C<sub>4</sub> macrophyte debris makes them available for being channeled through aquatic  
329 food webs. These findings can explain why Amazon food webs are mainly centered on a C<sub>3</sub>  
330 carbon source (Araujo-Lima et al., 1986; Hamilton et al., 1992; Forsberg et al., 1993),  
331 although C<sub>4</sub> macrophytes display a greater food quality and biomass for specialized herbivore  
332 fish species (Mortillaro et al., 2015).

333

### 334 **Conclusion**

335 Within the present experiment, the higher lability of C<sub>4</sub> compared to C<sub>3</sub> macrophytes was  
336 demonstrated. The contribution of *P. repens* to POC and DOC isotopes compositions reached  
337 a maximum after 3 to 6 days, indicating a fast decomposition rate of this macrophyte.  
338 Moreover, *P. repens* biomasses had a noticeable impact on OM composition. The  
339 decomposition of C<sub>4</sub> macrophytes was followed by the mineralization into DIC, as suggested  
340 by  $\delta^{13}\text{C}$ -DIC, as well as by the release of DIN and P. Therefore, the fast mineralization of C<sub>4</sub>  
341 macrophytes, as well as the natural mixing of POM with <sup>13</sup>C-depleted primary producers (e.g.  
342 phytoplankton, C<sub>3</sub> macrophytes, periphyton, and trees), should account for the overall low  
343 contribution of C<sub>4</sub> carbon sources to the central Amazon aquatic food webs.

344

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356

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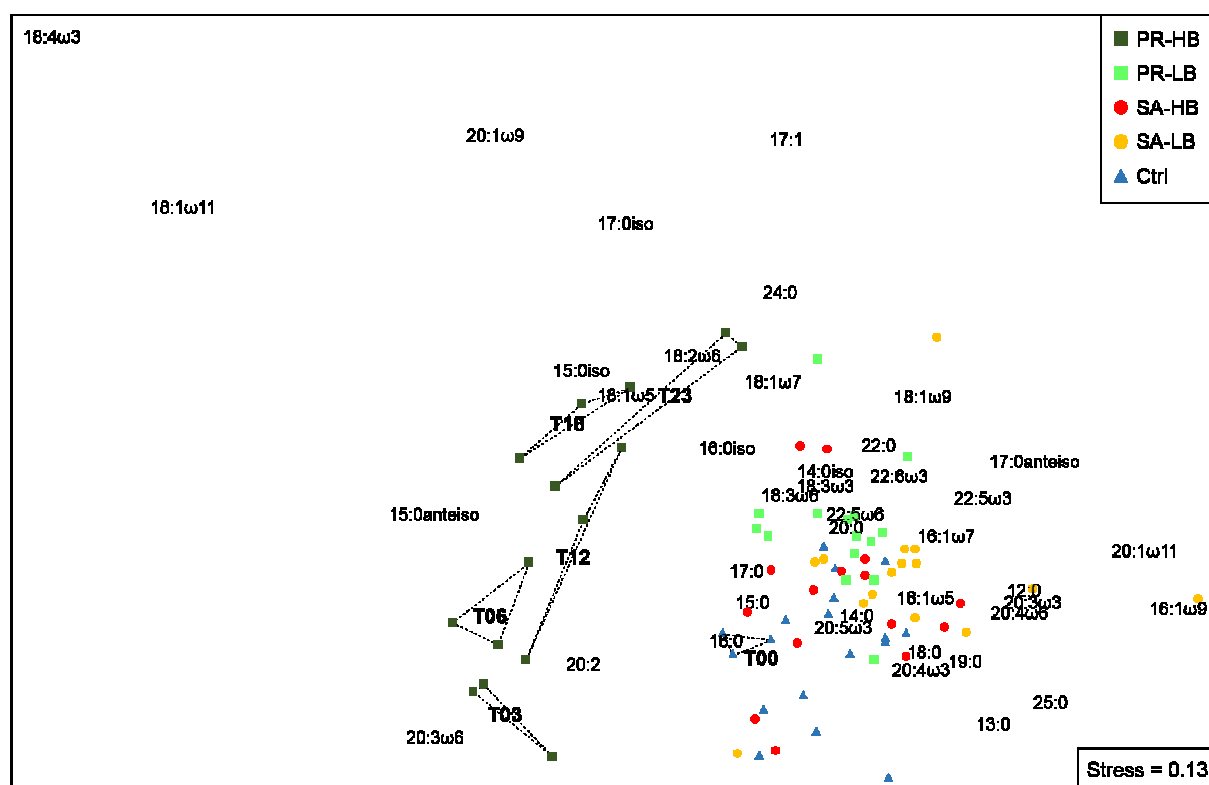
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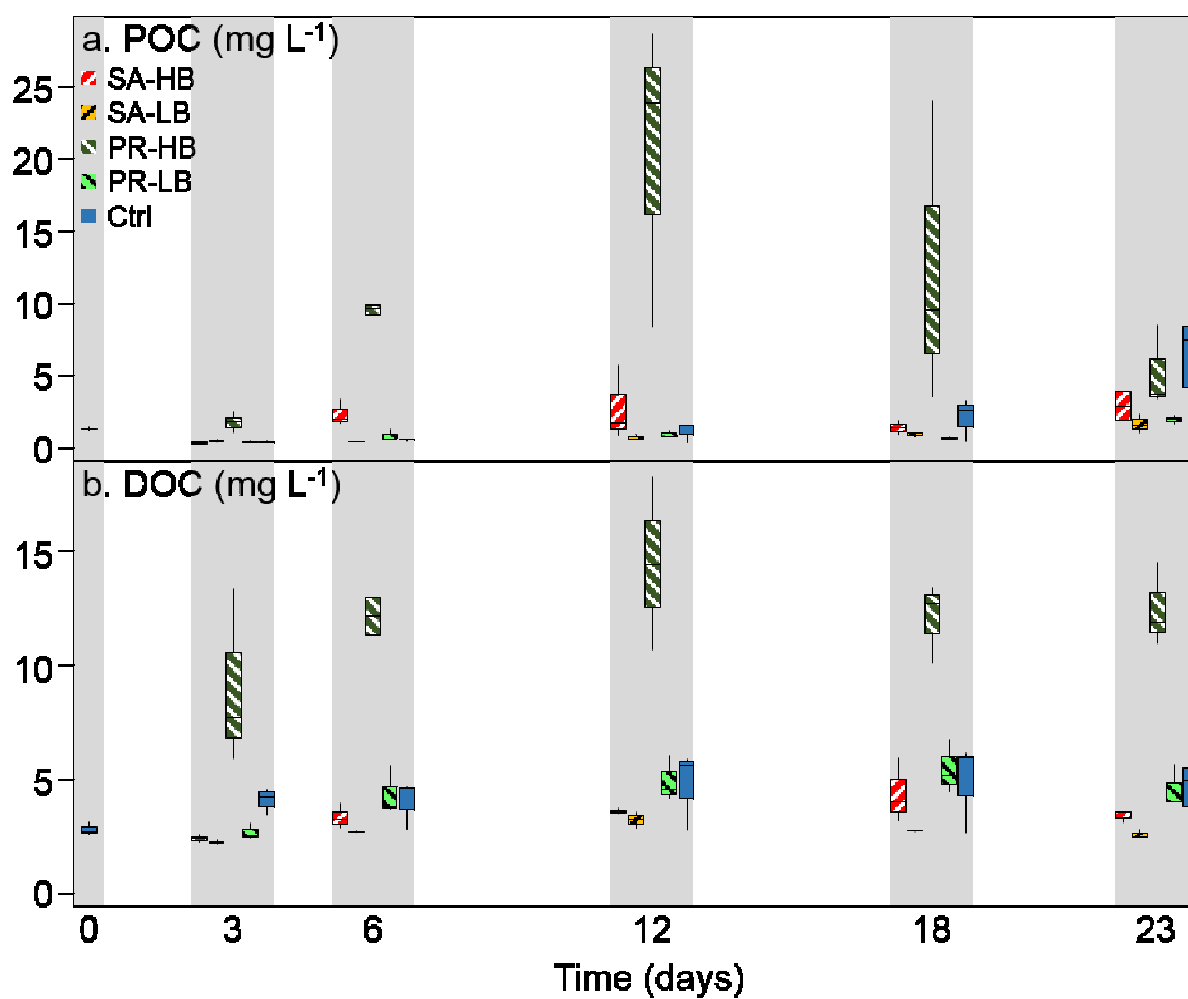
530 Fig. 1. Floating meadows of *P. repens* (left) and *S. auriculata* (right).

531



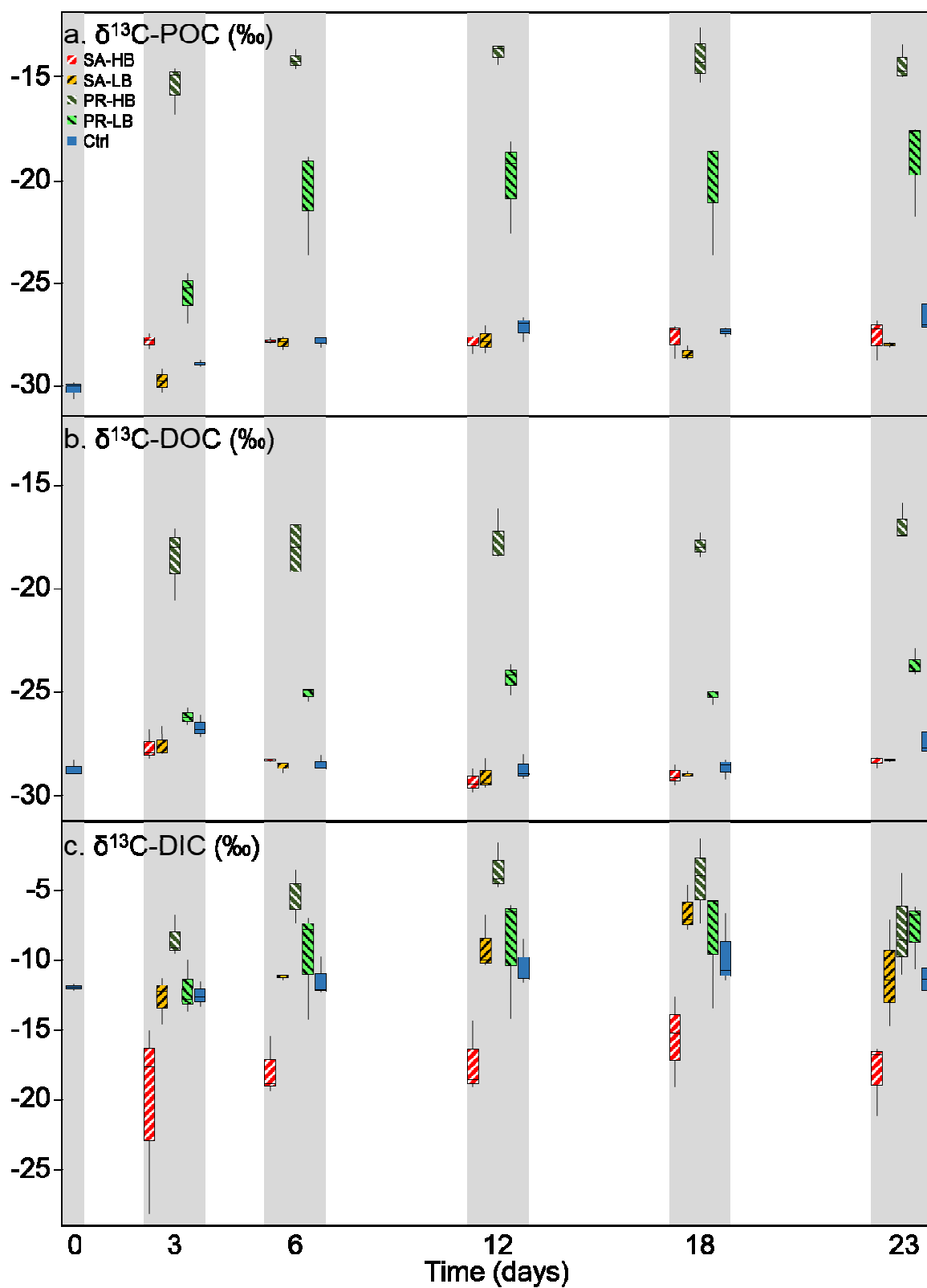
532

533 Fig. 2. Nonmetric MDS of FA proportions (%) in POM. Squares (■) are for *P. repens*  
 534 treatments with high (dark green) and low (light green) biomasses, circles (●) are for  
 535 *S. auriculata* treatments with high (red) and low (orange) biomasses and blue triangles (▲)  
 536 are for the Ctrl treatment.



537

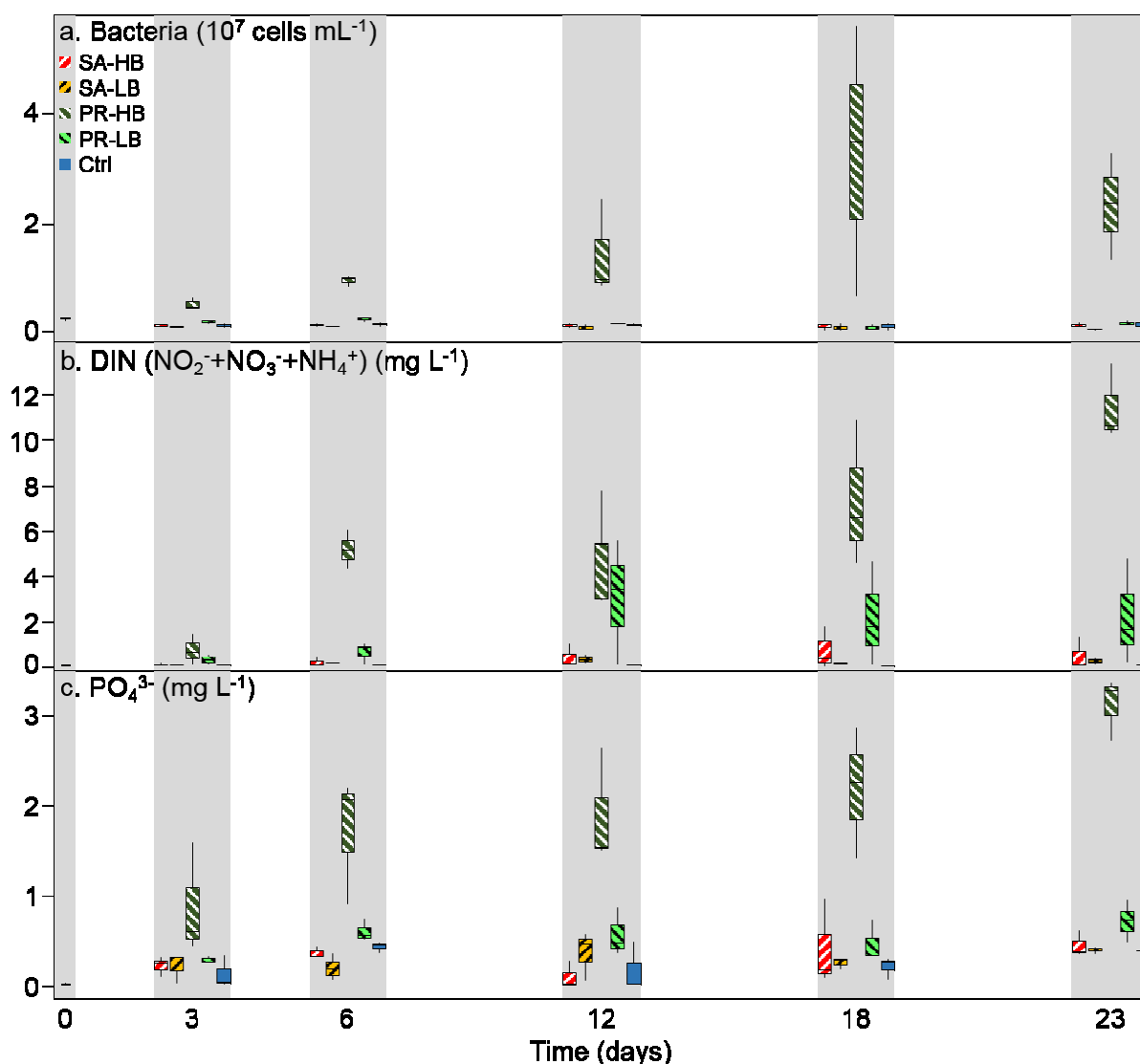
538 Fig. 3. Boxplot of POC (a.) and DOC (b.) concentrations in each treatment: PR-HB (dark  
 539 green), PR-LB (light green), SA-HB (red), SA-LB (orange) and Ctrl (blue). Note that DIC  
 540 time-courses were not determined because of the CO<sub>2</sub> loss to the atmosphere occurring  
 541 throughout the experiment.



542

543 Fig. 4. Boxplot of  $\delta^{13}\text{C}$ -POC (a.),  $\delta^{13}\text{C}$ -DOC (b.)  $\delta^{13}\text{C}$ -DIC (c.) in each treatment: PR-HB

544 (dark green), PR-LB (light green), SA-HB (red), SA-LB (orange) and Ctrl (blue).



545  
 546 Fig. 5. Boxplot of bacteria abundances (a.), DIN (b.) and  $\text{PO}_4$  (c.) concentrations in each  
 547 treatment: PR-HB (dark green), PR-LB (light green), SA-HB (red), SA-LB (orange) and Ctrl  
 548 (blue).

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552 Table 1. FA concentrations and stable isotope compositions ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) of POM  
 553 (FA:  $\mu\text{g L}^{-1}$ ) and macrophytes (FA:  $\text{mg g}^{-1}$ ) collected in Camaleão várzea. In bold are the  
 554 proportion of saturated (SFA), branched (BFA), monounsaturated (MUFA), polyunsaturated  
 555 (PUFA) and long chain FA (LCFA).

	POM ( $\mu\text{g L}^{-1}$ )	<i>P. repens</i> ( $\text{mg g}^{-1}$ )	<i>S. auriculata</i> ( $\text{mg g}^{-1}$ )
FA	n=3 $\pm$ S.D.	n=3 $\pm$ S.D.	n=3 $\pm$ S.D.
12:0	2.25 $\pm$ 1.81	0.10 $\pm$ 0.02	0.03 $\pm$ 7 $10^{-3}$
13:0	0.39 $\pm$ 0.10	1 $10^{-3}$ $\pm$ 5 $10^{-4}$	5 $10^{-3}$ $\pm$ 1 $10^{-3}$



14:0	6.13 ± 1.61	0.10 ± 4 10 <sup>-3</sup>	0.20 ± 0.05
15:0	2.25 ± 0.34	0.03 ± 2 10 <sup>-3</sup>	0.06 ± 0.01
16:0	24.14 ± 3.95	3.69 ± 0.38	2.33 ± 0.28
17:0	0.75 ± 0.10	0.11 ± 0.01	0.05 ± 0.01
18:0	5.54 ± 1.83	0.74 ± 0.12	0.22 ± 0.05
19:0	0.31 ± 0.02	4 10 <sup>-3</sup> ± 2 10 <sup>-3</sup>	7 10 <sup>-3</sup> ± 1 10 <sup>-3</sup>
20:0	0.30 ± 0.09	0.19 ± 0.03	0.02 ± 5 10 <sup>-3</sup>
22:0	0.38 ± 0.14	0.37 ± 0.07	0.04 ± 4 10 <sup>-3</sup>
<b>%SFA</b>	<b>78.84 ± 1.76</b>	<b>43.77 ± 4.67</b>	<b>80.35 ± 3.23</b>
14:0iso	0.55 ± 0.13	0.08 ± 0.02	2 10 <sup>-3</sup> ± 1 10 <sup>-3</sup>
15:0anteiso	0.78 ± 0.15	0.05 ± 0.02	0.01 ± 1 10 <sup>-3</sup>
15:0iso	2.67 ± 0.68	0.06 ± 0.02	0.07 ± 5 10 <sup>-3</sup>
16:0iso	0.49 ± 0.12	4 10 <sup>-3</sup> ± 2 10 <sup>-3</sup>	0.02 ± 3 10 <sup>-3</sup>
17:0anteiso	0.58 ± 0.18	3 10 <sup>-3</sup> ± 8 10 <sup>-4</sup>	0.01 ± 2 10 <sup>-3</sup>
17:0iso	0.56 ± 0.13	0.21 ± 0.04	0.04 ± 0.01
<b>%BFA</b>	<b>10.43 ± 0.76</b>	<b>3.23 ± 0.10</b>	<b>3.98 ± 0.18</b>
16:1ω5	0.22 ± 0.03	0.01 ± 4 10 <sup>-3</sup>	0.02 ± 6 10 <sup>-4</sup>
16:1ω7	0.36 ± 0.32	0.02 ± 5 10 <sup>-3</sup>	0.01 ± 0.02
16:1ω9	0.13 ± 0.07	0.28 ± 0.11	4 10 <sup>-3</sup> ± 3 10 <sup>-3</sup>
17:1	0.16 ± 0.06	0.01 ± 0.01	0.01 ± 2 10 <sup>-3</sup>
18:1ω5	0.03 ± 0.00	n.d. ± n.d.	n.d. ± n.d.
18:1ω7	0.10 ± 0.04	0.06 ± 0.01	5 10 <sup>-3</sup> ± 6 10 <sup>-4</sup>
18:1ω9	0.01 ± 0.01	n.d. ± n.d.	n.d. ± n.d.
18:1ω9	n.d. ± n.d.	0.21 ± 0.04	2 10 <sup>-3</sup> ± 2 10 <sup>-3</sup>
20:1ω11	n.d. ± n.d.	2 10 <sup>-3</sup> ± 5 10 <sup>-4</sup>	n.d. ± n.d.
20:1ω9	n.d. ± n.d.	8 10 <sup>-3</sup> ± 3 10 <sup>-3</sup>	n.d. ± n.d.
<b>%MUFA</b>	<b>1.83 ± 0.35</b>	<b>4.79 ± 0.66</b>	<b>1.30 ± 0.07</b>
16:4ω3	n.d. ± n.d.	0.12 ± 0.02	0.01 ± 4 10 <sup>-3</sup>
18:2ω6	0.10 ± 0.08	1.34 ± 0.38	2 10 <sup>-3</sup> ± 9 10 <sup>-4</sup>
18:3ω3	0.12 ± 0.01	3.60 ± 1.07	0.01 ± 4 10 <sup>-3</sup>
18:3ω6	0.11 ± 0.06	4 10 <sup>-3</sup> ± 1 10 <sup>-3</sup>	0.08 ± 0.07
18:4ω3	n.d. ± n.d.	n.d. ± n.d.	1 10 <sup>-3</sup> ± 2 10 <sup>-3</sup>
20:2	0.13 ± 0.03	0.01 ± 4 10 <sup>-3</sup>	4 10 <sup>-3</sup> ± 2 10 <sup>-3</sup>
20:3ω3	0.54 ± 0.26	0.03 ± 0.00	0.01 ± 6 10 <sup>-3</sup>
20:3ω6	0.31 ± 0.10	0.01 ± 1 10 <sup>-3</sup>	0.04 ± 0.03
20:4ω3	0.34 ± 0.05	n.d. ± n.d.	3 10 <sup>-3</sup> ± 8 10 <sup>-4</sup>
20:4ω6	0.08 ± 0.02	0.02 ± 2 10 <sup>-3</sup>	3 10 <sup>-3</sup> ± 8 10 <sup>-4</sup>
20:5ω3	0.08 ± 0.01	4 10 <sup>-3</sup> ± 2 10 <sup>-4</sup>	9 10 <sup>-4</sup> ± 3 10 <sup>-4</sup>
22:5ω3	0.10 ± 0.04	4 10 <sup>-3</sup> ± 1 10 <sup>-3</sup>	3 10 <sup>-3</sup> ± 1 10 <sup>-4</sup>
22:5ω6	2.22 ± 0.43	0.04 ± 6 10 <sup>-3</sup>	0.05 ± 0.01
22:6ω3	0.39 ± 0.13	0.01 ± 6 10 <sup>-4</sup>	n.d. ± n.d.
<b>%PUFA</b>	<b>8.61 ± 1.67</b>	<b>41.57 ± 4.45</b>	<b>5.68 ± 2.40</b>
24:0	0.05 ± 7 10 <sup>-3</sup>	0.55 ± 0.11	0.20 ± 0.04
25:0	0.12 ± 0.01	0.04 ± 5 10 <sup>-3</sup>	0.02 ± 6 10 <sup>-3</sup>
26:0	n.d. ± n.d.	0.23 ± 0.06	0.10 ± 0.03
<b>%LCFA</b>	<b>0.28 ± 0.02</b>	<b>6.65 ± 0.57</b>	<b>8.69 ± 0.91</b>
δ <sup>13</sup> C (‰)	-30.15 ± 0.43	-13.02 ± 0.81	-30.53 ± 0.51
δ <sup>15</sup> N (‰)	2.43 ± 0.71	4.01 ± 1.32	2.25 ± 1.11

556 n.d. = not detected

557

558 Table 2. Summary of ANOSIM pairwise tests for FA composition of POM between  
 559 treatments. Values in italics ( $R < 0.3$ ) are for high intragroup variability.

Groups	<i>R</i>	<i>p</i> value
PR-HB : Ctrl	0.80	$< 10^{-3}$
PR-HB : PR-LB	0.73	$< 10^{-3}$
PR-HB : SA-HB	0.75	$< 10^{-3}$
PR-HB : SA-LB	0.82	$< 10^{-3}$
PR-LB : Ctrl	0.27	$< 10^{-3}$
PR-LB : SA-HB	0.07	0.06 <sup>NS</sup>
PR-LB : SA-LB	0.11	$< 10^{-3}$
SA-HB : Ctrl	0.04	0.15 <sup>NS</sup>
SA-HB : SA-LB	0.04	0.11 <sup>NS</sup>
SA-LB : Ctrl	0.15	0.01

560 NS = non-significant

561 Table 3. Intragroup similarity of FA compositions in different treatments, and percentages of  
 562 FA explaining most of this similarity (SIMPER procedure).

Treatment (intragroup similarity)	14:0	15:0iso	15:0anteiso	15:0	16:0	18:0	22:5ω6	Σ (%)
PR-HB (77.3 %)	6.5	11.2	6.3	3.9	44.1	4.9	5.1	76.8
PR-LB (85.1 %)	8.7	6.8	1.6	3.7	33.7	12.7	4.5	73.7
SA-HB (82.6 %)	8.8	3.9	1.5	3.4	37.1	13.8	5.0	75.4
SA-LB (81.7 %)	9.4	3.4	1.4	3.5	33.0	13.2	4.0	71.7
Ctrl (83.7 %)	8.5	3.8	1.4	3.3	39.4	14.3	4.9	77.7

563

564 Table 4. Summary of KW and MWW pairwise tests for  $\delta^{13}\text{C}$ -POC,  $\delta^{13}\text{C}$ -DOC,  $\delta^{13}\text{C}$ -DIC;  
 565 POC, DOC, DIN,  $\text{PO}_4^{3-}$  concentrations and bacterial abundances of water samples between  
 566 treatments.

	$\delta^{13}\text{C}$ -POC	$\delta^{13}\text{C}$ -DOC	$\delta^{13}\text{C}$ -DIC	[POC]	[DOC]	[DIN]	$[\text{PO}_4^{3-}]$	Bact
KW Global test	$5 \cdot 10^{-7}$	$3 \cdot 10^{-8}$	$6 \cdot 10^{-9}$	$5 \cdot 10^{-6}$	$4 \cdot 10^{-6}$	$10^{-5}$	$10^{-6}$	$10^{-9}$
PR-HB : Ctrl	$7 \cdot 10^{-4}$	$3 \cdot 10^{-4}$	$8 \cdot 10^{-4}$	$1 \cdot 10^{-3}$	$1 \cdot 10^{-3}$	$1 \cdot 10^{-3}$	$2 \cdot 10^{-3}$	$< 10^{-4}$
PR-HB : PR-LB	$7 \cdot 10^{-4}$	$1 \cdot 10^{-3}$	0.03	$1 \cdot 10^{-4}$	$1 \cdot 10^{-3}$	0.05	$5 \cdot 10^{-3}$	$< 10^{-4}$
PR-HB : SA-HB	$7 \cdot 10^{-4}$	$2 \cdot 10^{-4}$	$< 10^{-4}$	$7 \cdot 10^{-3}$	$1 \cdot 10^{-3}$	$4 \cdot 10^{-3}$	$2 \cdot 10^{-3}$	$< 10^{-4}$
PR-HB : SA-LB	$7 \cdot 10^{-4}$	$2 \cdot 10^{-4}$	$9 \cdot 10^{-3}$	$1 \cdot 10^{-4}$	$2 \cdot 10^{-4}$	$4 \cdot 10^{-3}$	$2 \cdot 10^{-3}$	$< 10^{-4}$
PR-LB : Ctrl	$9 \cdot 10^{-4}$	$3 \cdot 10^{-4}$	0.44 <sup>NS</sup>	0.86 <sup>NS</sup>	0.71 <sup>NS</sup>	$2 \cdot 10^{-3}$	0.07 <sup>NS</sup>	0.15 <sup>NS</sup>
PR-LB : SA-HB	$7 \cdot 10^{-4}$	$2 \cdot 10^{-4}$	$< 10^{-4}$	0.05	0.06 <sup>NS</sup>	0.09 <sup>NS</sup>	0.06 <sup>NS</sup>	0.06 <sup>NS</sup>
PR-LB : SA-LB	$7 \cdot 10^{-4}$	$2 \cdot 10^{-4}$	0.59 <sup>NS</sup>	0.64 <sup>NS</sup>	$2 \cdot 10^{-3}$	0.13 <sup>NS</sup>	0.06 <sup>NS</sup>	0.01
SA-HB : Ctrl	0.60 <sup>NS</sup>	0.23 <sup>NS</sup>	$< 10^{-4}$	0.29 <sup>NS</sup>	0.11 <sup>NS</sup>	0.06 <sup>NS</sup>	0.90 <sup>NS</sup>	0.33 <sup>NS</sup>
SA-HB : SA-LB	0.11 <sup>NS</sup>	0.94 <sup>NS</sup>	$< 10^{-4}$	0.03	0.02	0.46 <sup>NS</sup>	0.90 <sup>NS</sup>	0.12 <sup>NS</sup>
SA-LB : Ctrl	0.08 <sup>NS</sup>	0.25 <sup>NS</sup>	0.38 <sup>NS</sup>	0.58 <sup>NS</sup>	$2 \cdot 10^{-3}$	$1 \cdot 10^{-3}$	0.90 <sup>NS</sup>	0.04

567 NS = non-significant.

568