Organic Geochemistry 42 (2011) 1159–1168

Contents lists available at SciVerse ScienceDirect

Organic Geochemistry

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

Fatty acid and stable isotope ($\delta^{13}C$, $\delta^{15}N$) signatures of particulate organic matter in the lower Amazon River: Seasonal contrasts and connectivity between floodplain lakes and the mainstem

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ARTICLE INFO

Article history:
Received 7 June 2011
Received in revised form 15 August 2011
Accepted 18 August 2011
Available online 24 August 2011

ABSTRACT

Fatty acid (FA) composition and stable isotope ($\delta^{13}C$, $\delta^{15}N$) signatures of four aquatic plants, plankton, sediment, soil and suspended particulate organic matter (SPOM) collected from open floodplain lakes (Várzea) and rivers of the central Brazilian Amazon basin were gathered during high and low water stages in 2009. SPOM from Várzea had a major contribution of autochthonous material from phytoplankton and C_3 aquatic plants. As shown from stable isotope composition of SPOM ($\delta^{13}C$ −31.3 ± 3.2‰; $\delta^{15}N$ 3.6 ± 1.5‰), the C_4 aquatic phanerogam ($\delta^{13}C$ −13.1 ± 0.5‰; $\delta^{15}N$ 4.1 ± 1.7‰) contribution appeared to be weak, although these plants were the most abundant macrophyte in the Várzea. During low water season, increasing concentration of 18:3ω3 was recorded in the SPOM of lakes. This FA, abundant mainly in the Várzea plants (up to 49% of total FAs), was due to the accumulation of their detritus in the ecosystem. This dry season, when connectivity with the river mainstem was restricted, was also characterized by a high concentration in the SPOM of the cyanobacteria marker 16:1ω7 (up to 21% of total FAs). The FA compositions of SPOM from the Amazon River also exhibited significant seasonal differences, in particular a higher concentration of 16:1ω7 and 18:3ω3 during the dry season. This suggests a seasonal contribution of autochthonous material produced in Várzea to the Amazon River SPOM.

1. Introduction

The transport of carbon by rivers is an important and well documented component of the global carbon cycle (Ludwig et al., 1996; Cole et al., 2007). Distinction is generally made between the organic and inorganic species, which account for 40% and 60%, respectively, of the 0.9×10^{15} g C y^{-1} carried every year by the world's rivers (Meybeck, 1993). Sources of organic carbon (OC) include input such as soil, production by heterotrophic organisms and assimilation by phytoplankton and periphyton (Barth and Veizer, 1999; Duarte and Prairie, 2005). However, their relative contributions to the total flux have not been fully evaluated (Bianchi and Allison, 2009) and are needed to assess the lateral exchange of organic carbon between ecosystems (Bouillon and Connolly, 2009).

The Amazonian basin is the largest river system on Earth, draining >6×10^6 km^2, contributing to up to 20% of all river discharge to the oceans (Sioli, 1984; Goulding et al., 2003). In the Amazon River system, CO_2 degassing has been estimated at 0.47×10^{15} g C y^{-1} (Richey et al., 2002), more than half Meybeck's (1993) calculations worldwide, and comparable with the estimated CO_2 released through deforestation and carbon sink by pristine forest in the Amazonian basin (Malhi et al., 2008). Characterization of inputs to the Amazon have identified transport of unreactive and highly degraded OM from upstream sources within the Solimões and Madeira rivers (Hedges et al., 1986; Aufdenkampe et al., 2007). However, Mayorga et al. (2005) analyzed ^{14}C in the CO_2 from the Amazon and showed that most of it originated from rapid recycling of young OC.

Large parts of the Amazon River are subjected to periodical floods in the surrounding central Amazon area, due mainly to spatial and temporal distribution of rainfall in the headwaters (Junk, 1997). This creates large temporary wetlands called Várzea, which account with rivers for a total area of ca. 350,000 km^2 (Melack and Hess, 2010). A lateral contribution from Várzea of labile OM (Moreira-Turcq et al., 2003) has also been identified, as suggested by Martinelli et al. (2003), with large stretches of the river margin falling into the river during the flood period. This suggests,

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doi:10.1016/j.orggeochem.2011.08.011

therefore, that the pool of OC produced in the Várzea is responsible for the large carbon flux from land to water and atmosphere in the Amazonian basin.

The fatty acid (FA) composition of OM has been successfully used to detail food web relationships (Dalsgaard et al., 2003; Hall et al., 2006; Nerot et al., 2009) and to differentiate (i) bacteria and fungi in soil (Frostegard and Baath, 1996) and (ii) phytoplankton and macroalgae in sediments (Meziane et al., 1997, 2006; Hu et al., 2006) and (iii) allochthonous and autochthonous particulate OM (Xu and Jaffe, 2007; Bechtel and Schubert, 2009). The FA composition of suspended particulate organic matter (SPOM) in the Amazon River has revealed a contribution from an unreactive and highly degraded OM component (Saliot et al., 2001).

Other markers, such as the natural $\delta^{13}C$ and $\delta^{15}N$ signatures, have been widely used to elucidate the source and fate of OM within aquatic environments (Gu et al., 1994; Kaiser et al., 2003; Hunsinger et al., 2010), to characterize nutrient utilization by autotrophs (Teranes and Bernasconi, 2000) and to describe food web topology (Vander Zanden and Rasmussen, 2001; Riera and Hubas, 2003). Isotopic ratios of carbon and nitrogen can also be helpful in distinguishing between aquatic and terrestrial primary producers. However, their respective isotopic signals can be difficult to reveal in freshwater areas that receive varying contributions of OM from different photosynthetic sources such as phytoplankton or C_3 and C_4 terrestrial and aquatic plants from the Amazon basin (Hedges et al., 1986; Townsend-Small et al., 2005).

The aims of the present study were to (i) characterize OM in both Várzea and rivers by investigating FA composition and isotopic signatures in aquatic plants, soil, sediments, plankton samples and particulate OM, (ii) follow the seasonal flooding impact on the quality of particulate OM and (iii) trace connectivity between lakes and rivers in the Amazon ecosystem.

2. Material and methods

2.1. Study area

Three types of water occur throughout the Amazon River basin: white water, black water and clear water (Sioli, 1984). In the upper part of the basin, the Solimões and Madeira rivers, the main tributaries of the Amazon, are white water rivers with high dissolved and particulate concentrations as a result of the vast amount of nutrient-rich sediment carried from the Andes (Stallard and Edmond, 1983; Sioli, 1984). Rivers draining only the low relief and forested areas are either "black water" or "clear water" rivers, with low inorganic dissolved content and low suspended particle concentration (Gibbs, 1967). The Negro River water is "black" and, originating in the lowest Amazonian terrain and wetlands generally dominated by podzol soil, is loaded with OM in colloidal suspension and intensely colored by humic matter (Stallard and Edmond, 1983). The clear waters of the Tapajòs River are relatively transparent and green colored, originating in the Precambrian Shields with a related catchment area that has no podzol, being are neither turbid with detrital material nor colored by humic compounds (Sioli, 1984; Konhauser et al., 1994).

Samples were collected on a ca. 800 km transect along the lower Amazon River basin from Manacapuru on the Solimões River, to Santarem at the mouth of the Tapajós River, located in a gradient of decreasing flooded forest area and increasing open lake area (Fig. 1). The main channels of five rivers were selected (Solimões, Negro, Madeira, Amazon and Tapajós; Table 1) as well as five Várzea (Cabaliana, Janauacá, Canaçari, Miratuba and Curuaï; Table 1).

Two cruises were conducted in June 2009 during the high water season (HW) and October 2009 one month before the lowest water stage, referred to here as the low water season (LW). In June, as the water level was the highest in the last century, the study area was extensively inundated, enhancing exchange and mixing between the river mainstem, the flooded forest and the open floodplain lakes. In October, the water level was minimal, allowing little interaction with the main channel. The difference in water level at Obidos between HW and LW was 6 m; the amplitude is generally 3–4 m more upstream near Manaus (Sioli, 1984).

2.2. Sample collection and preparation

Leaves and roots of four macrophyte species were collected in HW, whereas no macrophytes were found during LW, as observed by Junk (1985). The four species were *Eichornia* sp. (water hyacinth), *Paspalum repens* (water paspalum), *Pistia stratiotes* (water lettuce) and *Salvinia auriculata* (eared watermoss). The vegetation consists of floating grasses that form floating mats or "meadows" (Junk and Howard-Williams, 1984). These species have been characterized as C_3 aquatic plants, except for *P. repens* which is a C_4 species.

Plankton nets of 20 μm and 63 μm mesh size were used to collect particulate OM within the Várzea. The nets were dragged (10 min) from a small boat at 3 km h^{-1} maximum speed. From the sediment collected from Várzea using a Van Veen grab of 1000 cm^2, only the first superficial 1 cm was sampled. Soils samples were collected in the non-flooded area using a gardening trowel. The first 2 cm were removed in order to eliminate dead leaves and other detrital material.

SPOM samples were collected using a Niskin bottle and filtered immediately through glass fiber filters (Whatman GF/F, porosity 0.7 μm, 47 mm diam.) using a vacuum system, under low pressure. The filters were pre-combusted at 450 °C for 12 h and individually weighed. SPOM samples were also collected from the rivers' mainstem, with one station repeated in HW and LW seasons for the Negro, Solimões, Madeira and Tapajós rivers, and four stations along the Amazon mainstem in both seasons (Table 1).

Three replicate were collected at each station and all samples were frozen (−20 °C) on the research vessel and transported frozen to France for lipid analysis.

2.3. FA extraction and analysis

Samples were processed following a slightly modified version of Bligh and Dyer (1959) as in Meziane et al. (2007). Lipids were extracted via ultrasonication for 20 min with distilled water:-$CHCl_3$:MeOH (1:1:2, v:v:v). An internal standard (23:0 FA: 10 μg) was introduced to the samples before extraction. The addition of a distilled water:$CHCl_3$ mixture (1:1, v:v) formed a two layer system enhanced by way of centrifugation (3000 rpm, 5 min). The lower $CHCl_3$ phase containing the lipids was retained, concentrated under a N_2 flow, and the residue saponified under reflux (90 min, 90 °C) with 2 mol NaOH:MeOH (1:2, v:v). Saponification and methylation were according to Meziane and Tsuchiya (2002) in order to obtain the total lipids as methyl esters. The FAs were separated and quantified by way of gas chromatography (GC; Varian CP-3800 equipped with flame ionization detector). Separation was performed using a Supelco OMEGAWAX 320 column (30 m × 0.32 mm i.d., 0.25 μm film thickness) with H_2 as carrier gas. After injection of 1 μl of sample at 60 °C, the temperature was raised to 150 °C at 40 °C min^{-1}, then to 240 °C (held 14 min) at 3 °C min^{-1}. Most FA peaks were identified by comparing their retention times with those of authentic standards (Supelco™ 37, PUFA-1 Marine Source, and Bacterial Mix; Supelco Inc., Bellefonte, PA, USA). For some samples, peaks of FAs were confirmed with GC–mass spectrometry (GC–MS; ThermoFinnigan TRACE DSQ). FAs are designated as $X{:}Y\omega Z$, where X is the number of carbons, Y the

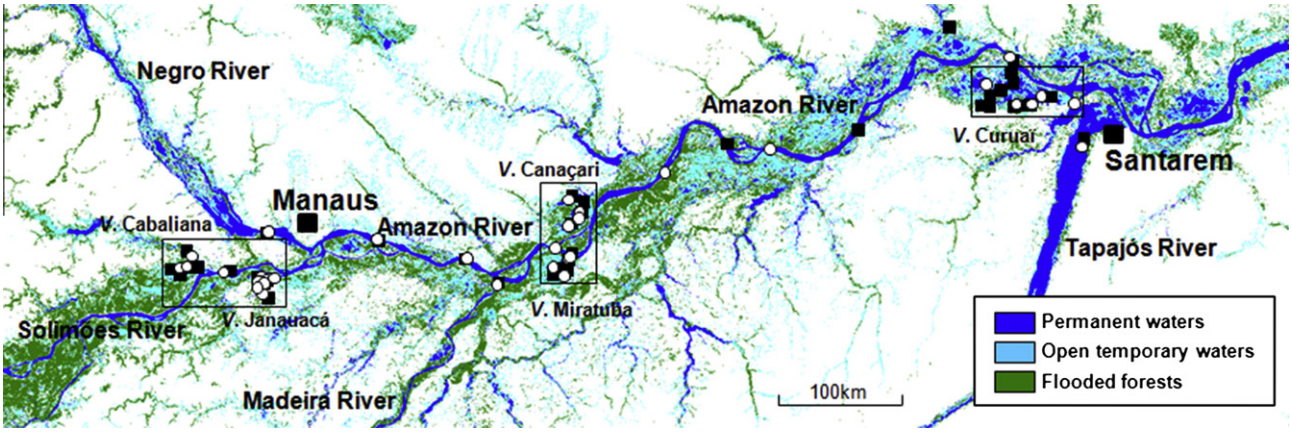

Fig. 1. Sampling sites on the Amazonian Basin (Brazil). Framed areas highlight the different Várzea. For each station, black squares are for HW and white circles for LW. Based on Martinez and Le Toan (2007).

Table 1
Conductivity, depth and suspended particulate matter (SPM) of Várzea and rivers sampled during high water (HW) and low water (LW).[a]

	HW (June 2009)				LW (October 2009)			
	Stations (n)	Conductivity (μS)	Depth (m)	SPM (mg l^{-1})	Stations (n)	Conductivity (μS)	Depth (m)	SPM (mg l^{-1})
Várzea								
Cabaliana	2	74 ± 1	14.1 ± 0.05	4.1 ± 0.2	2	75 ± 5	11 ± 5.5	6.7 ± 1.3
Janauacá	3	42 ± 2	13.1 ± 1.2	7.1 ± 0.5	3	59 ± 12	4.6 ± 1.7	9.4 ± 4.2
Mirituba	3	47 ± 4	10.4 ± 1.4	26.7 ± 5.2	3	55 ± 2	4.6 ± 1.7	60.3 ± 27.1
Camaçari	3	42 ± 9	11.1 ± 1.4	8.8 ± 4.2	4	44 ± 0	3.8 ± 1.4	23.2 ± 9.7
Curuaï	6	45 ± 2	8.3 ± 1	15.7 ± 5.1	3	45 ± 5	2 ± 0.2	53.4 ± 25.1
Rivers								
Negro	1	12 ± 0		2.3 ± 0.3	1	8 ± 0		4.5 ± 1.4
Solimões	1	71 ± 0		25.5 ± 1.3	1	76 ± 0		60.6 ± 2.6
Amazon	4	52 ± 5		16.4 ± 7	4	63 ± 3		36.9 ± 6.2
Madeira	1	41 ± 0		67.9 ± 6.1	1	77 ± 0		41.2 ± 1.7
Tapajós	1	18 ± 0		3 ± 0.6	1	18 ± 0		2.8 ± 0.4

[a] Data are mean (n) ± S.D.

number of double bonds and Z the position of the ultimate double bond from the terminal methyl.

The concentration of each FA (C_{FA} $mg_{of\ FA}/g_{of\ dry\ weight}$) was calculated according to Schomburg (1987):

$$C_{FA} = A_S/A_{IS} \times C_{IS}/W_S$$

where A_S is the peak area of the FA, A_{IS} the peak area of the internal standard, C_{IS} the concentration of the internal standard (mg) and W_S the dry weight of sample (g).

2.4. Stable isotopes

The isotopic ratio (R) values of dried samples ($^{13}C/^{12}C$ or $^{15}N/^{14}N$) were determined at the UC Davis Stable Isotope Facility (Department of Plant Sciences, University of California at Davis, Davis, California) using a Europe Hydra 20/20 mass spectrometer equipped with a continuous flow isotope ratio monitoring (IRM) device and are reported in standard delta notation ($\delta^{13}C$ or $\delta^{15}N$), defined as parts per thousand (‰) deviation from a standard (Vienna Peedee belemnite for $\delta^{13}C$ and atmospheric N_2 for $\delta^{15}N$) (Peterson and Fry, 1987):

$$\delta^{13}C \text{ or } \delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 1000$$

The analytical precision (standard deviation for repeated measurements of the internal standards) for the measurement was 0.06‰ and 0.13‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively.

2.5. Data analysis

The PRIMER 5 software was used for multivariate analysis (Clarke, 1993). The data matrices (% of total FAs) were used to create triangular similarity matrices, based on Bray–Curtis similarity coefficient. All FAs were used in the analyses and no transformation was performed on the data. Differences in FA composition among factors were tested using separate one-way analysis of similarity (ANOSIM) and the statistic test was computed after 5000 permutations. Factors used for the analysis where tissue (two levels: leaves and roots) and species (four levels, *Eichornia* sp., *P. repens*, *P. stratiotes* and *S. auriculata*) for macrophyte samples, and season (two levels: HW and LW) for plankton net, sediment and SPOM samples. The size of the mesh was used as another factor for plankton net samples (two levels: 63 and 20 μm). Where differences in FA composition were detected, similarity of percentage (SIMPER) tests, a module of PRIMER 5, were used to determine which FAs drove the differences between two sets of data. Temporal variation in FA composition of plankton samples, sediments and SPOM was displayed separately for each area using non-metric multi-dimensional scaling (MDS) plots based also on Bray–Curtis similarity measures.

Differences in concentration of selected individual FAs as well as $\delta^{13}C$ and $\delta^{15}N$ stable isotope signatures vs. season were tested using one-way analysis of variance (ANOVA) and the student t-test. The FAs selected for analysis of variance included those identified by way of SIMPER. Prior to ANOVA, all data were Box and Cox

(1964) transformed and tested for homoscedasticity (Levene and Bartlett tests) and normal distribution of residuals (Shapiro–Wilk and Jarque–Bera tests). Tukey's HSD Post-hoc tests were then used to determine the differences between groups. ANOVAs were performed using the XLSTAT-Pro 2010 software and for all tests the probability α was set at 0.05.

3. Results

3.1. FAs in macrophytes

The FA composition of the macrophytes species is summarized in Table A1 in the Appendix. Up to 38 FAs were identified; 16:0, 16:1ω7, 18:2ω6 and 18:3ω3 contributed up to 73–84% of the total FA content of leaves of *P. repens*, *P. stratiotes* and *Eichornia* sp., whereas in roots, 14:0, 16:0, 16:1ω7 and 18:2ω6 contributed up to 67–71% of the total. ANOSIM analysis found significant differences between FA profiles (% of total FAs) for all species (R 0.16, p 0.041). Differences where found between *S. auriculata* and *P. repens* (R 0.3, p 0.032), *P. stratiotes* (R 0.34, p 0.026) and *Eichornia* sp. (R 0.27, p 0.05), while, *P. repens*, *P. stratiotes* and *Eichornia* sp. were not statistically different ($R < 0.1$, $p > 0.1$). Significant differences were also found between leaves vs. root samples (ANOSIM; R 0.49, $p < 0.001$). An average dissimilarity of ca. 35% (SIMPER analysis) was found between the profiles of leaf and root samples. The dissimilarity was mainly due to a greater contribution of 18:3ω3 and 18:2ω6 and a lower contribution of 14:0, 16:0, 16:1ω7 and 18:1ω9 to leaves than roots. Significant differences in concentration (mg g^{-1} dry wt.) of 18:2ω6 and 18:3ω3 were recorded with a 2-way ANOVA (Tissue × Species; F 63.7, $p < 0.0001$ and F 158.9, $p < 0.0001$). This results in higher concentration of 18:2ω6 in leaves than roots of *P. repens* and *P. stratiotes* (Tuckey's HSD; $p < 0.0001$ for both), while its concentration is higher in the roots of *S. auriculata* (Tuckey's HSD; $p < 0.0001$), and no difference was found for *Eichornia* sp. (Tuckey's HSD; p 0.9). In addition, for 18:3ω3, a higher concentration was found in leaves of all species (Tuckey's HSD; $p < 0.0001$) except *S. auriculata*, for which the higher concentration was in the roots (Tuckey's HSD; p 0.001). Amongst the species, the highest FA concentration was in the tissue of *S. auriculata* and *P. repens* (Table A1, Appendix).

3.2. FAs in plankton from Várzea (i.e. 63 μm and 20 μm)

The FA composition of 63 and 20 μm plankton net contents from Várzea are summarized in Table A2 in the Appendix. Up to 47 FAs were identified in both 63 and 20 μm samples; 14:0, 16:0, 16:1ω7, 18:0, 18:1ω7, 18:1ω9, 18:2ω6, 18:3ω3, 20:4ω6, 20:5ω3 and 22:6ω3 contributed from 78% to 79% of the total. A significant difference was found in the profiles (% of total FAs) of 63 and 20 μm between seasons (ANOSIM; R 0.19, p 0.009; Fig. 2). Regardless of season, significant differences in FA content were recorded between the 63 and 20 μm samples (ANOSIM; R 0.36, $p < 0.0001$). An average dissimilarity of ca. 27% between HW and LW (SIMPER analysis) was found. This was due to higher contributions of 14:0, 16:1ω9, 18:0, 18:1ω7, 18:1ω9, 20:4ω6 and 22:6ω3 and lower contributions of 16:0, 16:1ω7, 18:2ω6 and 18:3ω3 from HW to LW. ANOVA was also used on the concentration and higher amounts (mg g^{-1} dry wt.) of 16:0, 16:1ω7, 18:2ω6 and 18:3ω3 were recorded from HW to LW (ANOVA, Table 2), whereas no significant differences were found in concentration between 63 and 20 μm plankton.

3.3. FAs in Várzea sediments

The composition of superficial Várzea sediments is summarized in Table A3 in the Appendix. Up to 48 FAs were identified; 14:0, iso15:0, anteiso15:0, 15:0, 16:0, 16:1ω7, 18:0, 18:1ω7, 18:1ω9, 22:0, 24:0, 26:0 and 28:0 contributed from 71% to 66% of the total FA content during HW and LW respectively. A significant difference was found in the profiles between HW and LW (ANOSIM; R 0.25, $p < 0.0001$; Fig. 2). An average dissimilarity of ca. 25% (SIMPER analysis) was found in FAs. This was due to higher contributions of 14:0, 15:0iso, 16:0, 16:1ω9, 18:0, 18:1ω9 and 18:2ω6 and lower contributions of 16:1ω7, 22:0, 22:1ω9, 24:0, 26:0 and 28:0 in HW than LW. From HW to LW, there was a significant increase of 16:1ω7 and 22:1ω9 (1-way ANOVA; F 5.8, p 0.019 and F 83.2, $p < 0.0001$) and a significant decrease in 18:0 (1-way ANOVA; F 17.7, $p < 0.0001$) concentrations in the samples.

3.4. FAs in Amazonian soil

The composition of soil sampled along the cruise in LW is summarized in Table A4 in the Appendix. Up to 46 FAs were identified.

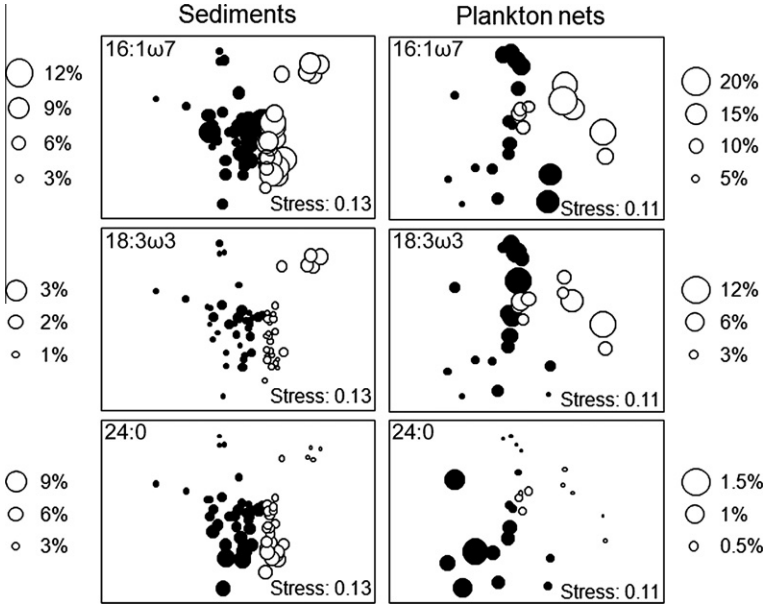

Fig. 2. Non-metric MDS of FA proportions from total FAs (%) in Várzea sediments and plankton samples from HW (black circles) and LW (white circles).

Table 2
Results of 2-way ANOVA comparing concentration of selected FAs among seasons and mesh size of plankton samples.

Plankton (63 and 20 μm)	16:0		16:1ω7		18:2ω6		18:3ω3	
Box–Cox (λ)	0.26		0.36		0.53		0.47	
Levenne's test	0.64^{NS}		0.048*		0.37^{NS}		0.44^{NS}	
Bartlett's test	0.37^{NS}		0.22^{NS}		0.78^{NS}		0.89^{NS}	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Season	5.94	0.020*	8.18	0.008*	10.67	0.003*	5.51	0.025*
Mesh size	0.02	0.896	0.11	0.744	1.02	0.321	1.04	0.315
Season × mesh size	0.01	0.926	0.02	0.882	0.10	0.754	0.48	0.493

F, Fisher; NS, not significant.
* $p < 0.05$.

An average similarity of ca. 70% (SIMPER analysis) was found. In these samples, 14:0, iso15:0, iso16:0, 16:0, 18:0, 18:1ω9, 18:3ω3, 20:0, 22:0, 22:1ω9, 24:0, 26:0 and 28:0 contributed up to 82% of the total FA content.

3.5. FAs in SPOM from Várzea

The composition of SPOM from Várzea waters is summarized in Table A5 in the Appendix. Up to 44 FAs were identified; 14:0, iso15:0, 15:0, 16:0, 16:1ω7, 16:1ω9, 17:0, 18:0, 18:1ω7, 18:1ω9, 18:2ω6, 18:3ω3, 18:4ω3 and 20:5ω3 contributed up to 85% of the total FA content during both HW and LW. Significant differences were found in the profiles between seasons (ANOSIM; *R* 0.61, $p < 0.0001$; Fig. 3). An average dissimilarity of ca. 29% (SIMPER analysis) was found between HW to LW. This was due to a higher contributions of 15:0, 16:1ω9, 18:0, 18:1ω7 and 18:1ω9 and a lower contribution of 14:0, 16:0, 16:1ω7, 18:2ω6 and 18:3ω3 during HW than LW. From HW to LW, significant increases in 14:0, iso15:0, 15:0, 16:0, 16:1ω7, 17:0, 18:0, 18:1ω7, 18:3ω3, 18:4ω3 and 20:5ω3 concentration were recorded (1-way ANOVA; Table 3).

3.6. Stable isotope signature of OM in Várzea

Aquatic plants showed $\delta^{13}C$ values typical of the C_3 photosynthetic pathway (up to −35‰) for *S. auriculata*, *P. stratiotes* and *Eichornia* sp. and a typical C_4 value for *P. repens* (−13‰), whereas $\delta^{15}N$ values showed a greater range of variation between species and tissue (2–5.6‰; Fig. 4). OM from soil sampled in LW exhibited $\delta^{13}C$ and $\delta^{15}N$ values of −27‰ and 6‰ respectively. OM of superficial sediment samples from HW to LW showed no difference in $\delta^{13}C$ and $\delta^{15}N$ signatures. Within planktonic samples (63 μm) from HW to LW, the $\delta^{15}N$ signature was depleted of ca. −3‰ (1-way ANOVA; *F* 43.3, $p < 0.0001$), whereas the $\delta^{13}C$ signature was enriched by ca. 4‰ (1-way ANOVA; *F* 7.8, $p < 0.008$; Fig. 4). Between HW and LW, SPOM samples showed no significant difference in $\delta^{13}C$ values (1-way ANOVA; *F* 3.5, *p* 0.065) due to a wider range of variation in $\delta^{13}C$ signature for LW, whereas a significant depletion was recorded for $\delta^{15}N$ (from 4.5‰ to 2.7‰ avg.; 1-way ANOVA; *F* 41.2, $p < 0.0001$; Fig. 4).

3.7. FAs in SPOM from rivers

The composition is summarized in Tables A6 and A7 in the Appendix. Between seasons, significant increases in different FAs

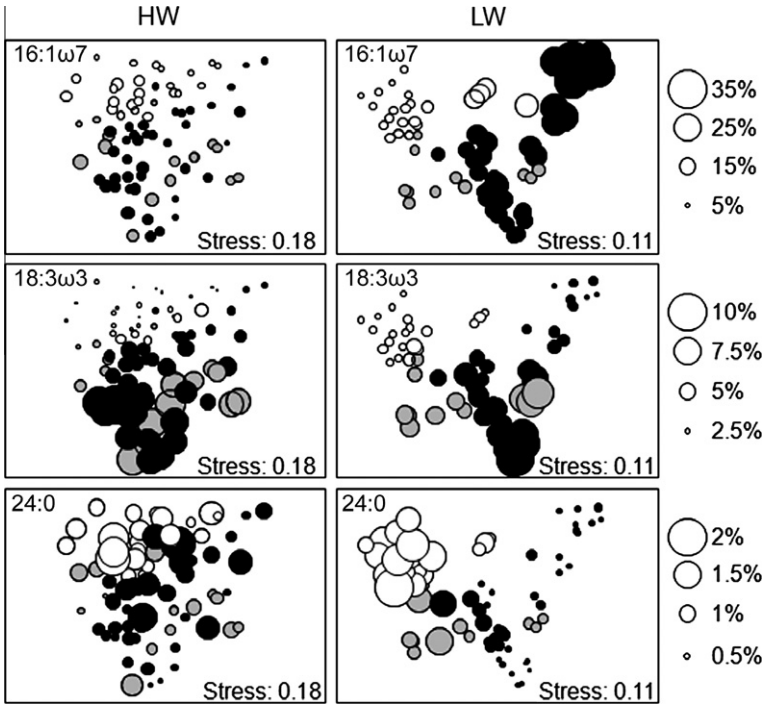

Fig. 3. Non-metric MDS of FA proportions from total FAs (%) in SPOM from Várzea (black circles), rivers of white water (white circles) and rivers of clear/black water (gray circles).

Table 3
Results of 1-way ANOVA comparing concentration of selected FAs between seasons inSPOM from Várzea.

SPOM	14:0		iso15:0		15:0		16:0	
Box–Cox (λ)	−0.09		−0.13		−0.34		0.11	
Levenne's test	0.26^{NS}		0.06^{NS}		0.05^{NS}		0.08^{NS}	
Bartlett's test	0.35^{NS}		0.16^{NS}		0.003^{*}		0.19^{NS}	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Season	97.05	$<0.001^{**}$	205.57	$<0.001^{**}$	10.61	0.002^{*}	140.72	$<0.001^{**}$
SPOM	16:1ω7		17:0		18:0		18:1ω7	
Box–Cox (λ)	−0.11		−0.10		−0.20		−0.03	
Levenne's test	0.11^{NS}		0.17^{NS}		0.41^{NS}		0.07^{NS}	
Bartlett's test	0.34^{NS}		0.11^{NS}		0.39^{NS}		0.08^{NS}	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Season	229.47	$<0.001^{**}$	8.90	0.004^{*}	5.53	0.021^{*}	58.14	$<0.001^{**}$
SPOM	18:3ω3		18:4ω3		20:5ω3			
Box–Cox (λ)	−0.01		−0.07		−0.18			
Levenne's test	0.001^{*}		0.35^{NS}		0.19^{NS}			
Bartlett's test	0.24^{NS}		0.21^{NS}		0.24^{NS}			
	F	*p*	*F*	*p*	*F*	*p*		
Season	77.25	$<0.001^{**}$	5.83	0.018^{*}	96.21	$<0.001^{**}$		

F, Fisher; NS, not significant.
* $p < 0.05$.
** $p < 0.001$.

were recorded (Table 4). These result mainly from a concentration increase from HW to LW for the two aquatic plant FAs, 18:2ω6 and 18:3ω3, in the Amazon, Solimões, Madeira and Negro rivers and 18:2ω6 for the Tapajós River (Table 4; Fig. 3). Also, a concentration increase in phytoplanktonic FAs was recorded, such as 14:0 for the Madeira River and 16:1ω7 for the Amazon, Madeira and Tapajós rivers (Table 4; Fig. 3).

3.8. Stable isotopes in SPOM from rivers

The stable isotope composition of SPOM sampled in both seasons along the rivers is summarized in Fig. 4. The $\delta^{13}C$ and $\delta^{15}N$ values range from −34‰ to −27‰ and from 1.6‰ to 6.6‰, respectively. Differences between seasons for water samples from the different rivers were tested using the Student *t*-test and showed a significant $\delta^{13}C$ enrichment for the Tapajós River (−33.8‰ to −26.7‰; *t*-test, *p* 0.016) during the LW stage. For the Solimões, Negro, Madeira and Amazon Rivers, no significant differences were recorded between seasons for both $\delta^{13}C$ and $\delta^{15}N$ ($p < 0.05$).

4. Discussion

4.1. OM sources

One of the most abundant plants of Várzea, *P. repens* but also *S. auriculata*, a C_4 and a C_3 aquatic plant respectively, showed the highest concentration of 18:2ω6 and 18:3ω3, as in other species of freshwater aquatic plants (Rozentsvet et al., 2002; Nesterov et al., 2009). These two FAs were detected in both roots and leaves of the aquatic plants, which account for a biomass of 6–23 t ha^{-1} in a floodplain lake (Junk and Piedade, 1993), and are therefore readily considered as the main sources of these two polyunsaturated FAs (PUFAs) in this environment. Characterization of the different OM sources showed that the SPOM $\delta^{13}C$ values were intermediate between those of C_3 aquatic plants, plankton, soil and sediments (Fig. 4). The SPOM was enriched in 18:2ω6 and 18:3ω3 (Fig. 3; Table A5 in Appendix). However, its $\delta^{13}C$ signature shows that there was only a weak contribution of OM derived from the C_4 aquatic phanerogam, such as *P. repens* and *Echinocloea polystachia*, although these plants are dominant in the biomass vs. C_3 species (Junk and Piedade, 1997). This low contribution suggests that C_4 plants are decomposed more rapidly than C_3 aquatic plants, a conclusion also reached by Quay et al. (1992) who analyzed the $\delta^{13}C$ composition of dissolved inorganic and OC in the Amazon River. To understand these differences in terms of contribution, further investigation of degradation processes for aquatic plants and dissolved OM is needed to assess the lack of a carbon enrichment in the SPOM resulting from the C_4 plants.

Planktonic samples (20 and 63 μm), as well as the SPOM from Várzea, were characterized by high proportions of 14:0, 16:0, 16:1ω7 and 20:5ω3 in both seasons (Figs. 2 and 3). Indeed, 16:1ω7 is a major, often prominent, FA constituent of some cyanobacteria (Murata et al., 1992) and diatoms (Sicko-goad et al., 1988; Pond et al., 1997). This was confirmed by microscopic observations (data not shown) showing a phytoplanktonic community dominated by cyanobacteria, as usually occurs in eutrophic lakes (Reynolds and Walsby, 1975).

Bacterial tracers (iso15:0, 15:0 and 17:0), that have been regularly described in bacterioplankton (Desvilettes et al., 1994; Hall et al., 2010), Gram-positive bacteria (Findlay and Dobbs, 1993; Mallet et al., 2004) and sulfate-reducing bacteria (Vainshtein et al., 1992; Findlay and Dobbs, 1993), were also recorded in all samples. The relationship between bacterial markers and unsaturated FAs (Tables A1–A7 in Appendix) is an indicator of the input of fresh natural OM (Saliot et al., 2001). The high proportions of monounsaturated FAs (MUFAs) and PUFAs, with respect to saturated (SFAs) and branched FAs (BFAs), suggest that mainly autochthonous material is decomposed by bacteria. This is consistent with the work of Waichman (1996), based on $\delta^{13}C$ analysis, which showed that heterotrophic bacteria use mainly autotrophic carbon sources such as aquatic macrophytes and phytoplankton.

Soils from Várzea and river banks were characterized by high proportions of long chain FAs (LCFAs) $\geqslant$ 24:0, which are synthesized solely by vascular plants (Cassagne et al., 1994) and thus attest, when present, to a terrestrial input to an aquatic ecosystem (Scribe et al., 1991; Colombo et al., 1996; Dunn et al., 2008). SPOM from the Amazonian basin bore a strong signature of vascular plants as has been described using FAs (Saliot et al., 2001) or lignin and amino acids (Hedges et al., 1994). In the SPOM from Várzea and river superficial waters, the proportion of LCFAs ranged from 0.53 ± 0.30% to 2.61 ± 0.55% (Fig. 3; Tables A5–A7 in Appendix). This therefore emphasizes a lesser influence of terrestrial OM in the SPOM from Várzea and the rivers than described with other

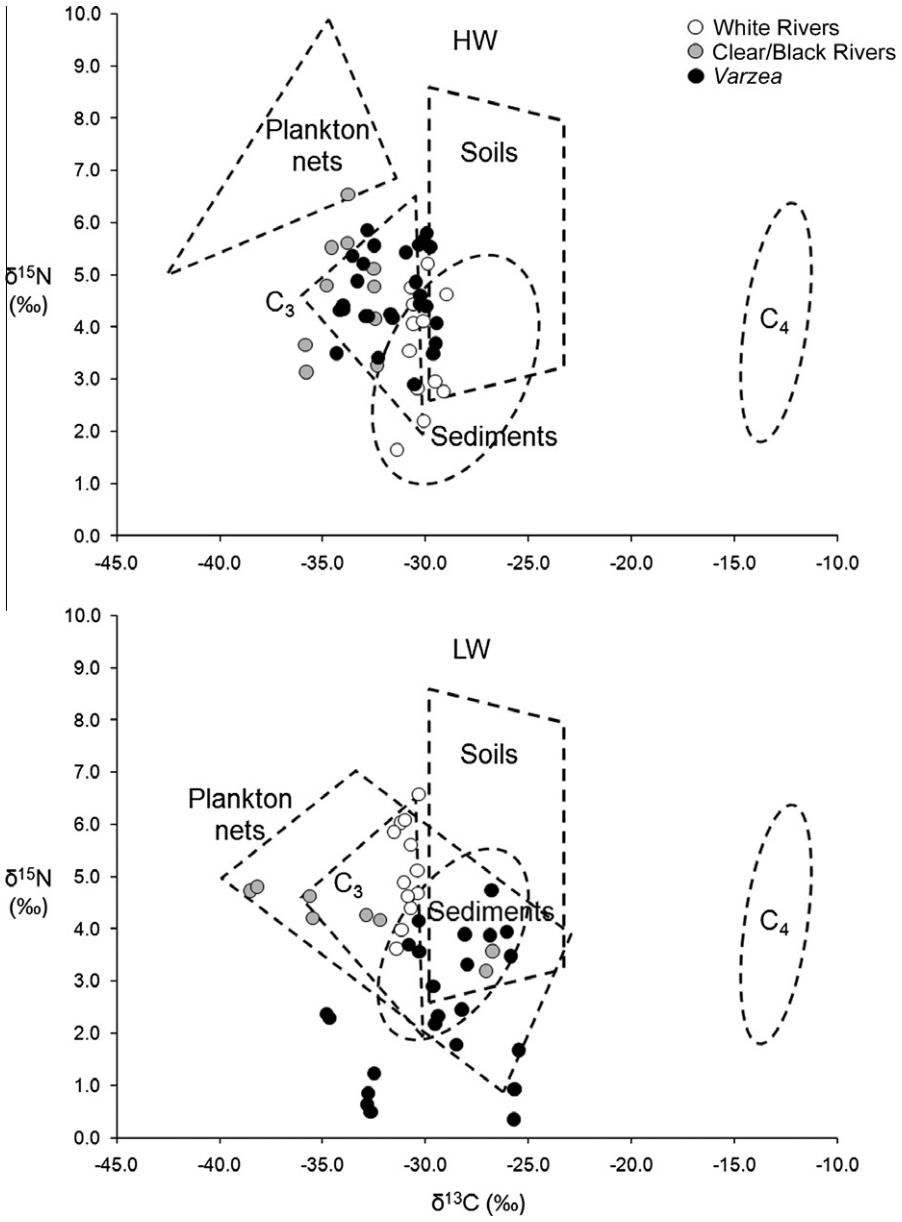

Fig. 4. A$\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) biplot of SPOM in Várzea (black circles) and rivers of white (white circles) and clear/black water (gray circles) in HW and LW. Each data point represents an individual sample. Dashed boxes represent the distribution of all points from soils, sediments, plankton, C_3 and C_4 aquatic plants.

proxies, with evidently a better contribution of autotrophic carbon sources. Others studies that focused on lignin in (Hernes et al., 2007), and ^{14}C signature of (Mayorga et al., 2005), dissolved OM demonstrated that it was derived from algal or microbial biomass and not from highly degraded vascular plants. In contrast, in the Várzea sediments, high proportions of LCFAs were recorded (Fig. 2; Table A3 in Appendix), suggesting selective preservation and degradation of the different sources of OM. Indeed burial of OM occurs in floodplains and consists mainly of terrestrial material adsorbed on particles carried by the Amazon River flood (Hedges et al., 1986; Moreira-Turcq et al., 2004).

Analysis of the SPOM sources in the Lower Amazon Basin, suggests a major contribution of autochthonous material derived from C_3 aquatic plants and phytoplankton. This was supported by calculated carbon budgets for the Amazon ecosystems (Quay et al., 1992; Melack et al., 2009), which indicated that net primary productivity of aquatic macrophytes within the floodplains accounts for a large fraction of the respired CO_2 within channels.

4.2. Seasonal contrasts

The 18:3ω3 enrichment of the Várzea SPOM during LW vs. HW (Table 3; Fig. 3) is mainly due to a higher contribution from macrophytes. However, biomass estimates of the Eastern Amazon floodplain by way of field measurements and remote sensing (Silva et al., 2009, 2010), point out a maximum value in June–July and a minimum in October–December, correlated with water column depth and submerged stem length. As the water level decreases, the macrophytes are subject to intensive degradation (Rai and Hill, 1984). This suggests that an increasing contribution of this specific FA marker to the SPOM results from the accumulation of detritus following the loss of plant biomass in the ecosystem during the receding water level.

In the SPOM, a significant seasonal increase during LW in FA concentration was mainly a result of phytoplankton (14:0, 16:1ω7, 18:4ω3 and 20:5ω3; Table 3). Indeed, during LW, both phytoplankton and zooplankton communities reach their

Table 4
Results of 1-way ANOVA comparing concentration of selected FAs between seasons inSPOM from rivers.

Amazon River	14:0		16:1ω7		18:2ω6		18:3ω3	
Box–Cox (λ)	0.01		0.01		0.55		0.14	
Levenne's test	0.07^{NS}		0.69^{NS}		0.29^{NS}		0.16^{NS}	
Bartlett's test	0.21^{NS}		0.88^{NS}		0.26^{NS}		0.04^{*}	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Season	0.70	0.410	6.57	0.015^{*}	45.02	$<0.001^{**}$	5.51	0.025^{*}
Solimões River	14:0		16:1ω7		18:2ω6		18:3ω3	
Box–Cox (λ)	0.01		−2.63		0.29		0.81	
Levenne's test	0.19^{NS}		0.45^{NS}		0.42^{NS}		0.56^{NS}	
Bartlett's test	0.34^{NS}		0.67^{NS}		0.68^{NS}		0.71^{NS}	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Season	0.34	0.59	0.63	0.47	25.61	0.007^{*}	31.45	$<0.001^{**}$
Madeira River	14:0		16:1ω7		18:2ω6		18:3ω3	
Box–Cox (λ)	−0.47		0.01		0.48		0.26	
Levenne's test	0.80^{NS}		0.63^{NS}		0.21^{NS}		0.27^{NS}	
Bartlett's test	0.87^{NS}		0.79^{NS}		0.40^{NS}		0.29^{NS}	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Season	20.99	0.010^{*}	34.29	0.004^{*}	30.14	0.005^{*}	65.18	0.001^{*}
Negro River	14:0		16:1ω7		18:2ω6		18:3ω3	
Box–Cox (λ)	0.53		−2.58		−1.58		−0.12	
Levenne's test	0.11^{NS}		0.79^{NS}		0.28^{NS}		0.86^{NS}	
Bartlett's test	0.08^{NS}		0.89^{NS}		0.55^{NS}		0.96^{NS}	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Season	0.11	0.76	2.53	0.190	14.22	0.020^{*}	22.91	0.009^{*}
Tapajós River	14:0		16:1ω7		18:2ω6		18:3ω3	
Box–Cox (λ)	2.98		0.01		1.59		−4.23	
Levenne's test	0.36^{NS}		0.17^{NS}		0.09^{NS}		0.15^{NS}	
Bartlett's test	0.61^{NS}		0.43^{NS}		0.26^{NS}		0.31^{NS}	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Season	2.18	0.210	24.46	0.008^{*}	25.97	0.007^{*}	20.28	0.011^{*}

F, Fisher; NS, not significant.
* $p < 0.05$.
** $p < 0.001$.

maximum standing stock in the floodplain lakes, which correlates with an increase in SPOM, due to the resuspension of bottom sediments into the water column by wind action (Carvalho, 1981). In addition, a high amount of 18:1ω7 from LW, associated with cyanobacteria biomass in a similar ecosystem (Goodloe and Light, 1982; Ahlgren et al., 1992), indicates that such phytoorganisms are a major contributor to the SPOM rather than the other planktonic communities. The significant depletion in $\delta^{15}N$ values from HW to LW in plankton samples (63 μm) and SPOM could be partly due to atmospheric N_2 fixation ($\delta^{15}N_{atm}$ 0‰) by the cyanobacteria (Fiore et al., 2005; Gu, 2009). Moreover, as for $\delta^{15}N$ depletion, the significant enrichment of 4‰ in $\delta^{13}C$ values for plankton samples (63 μm; Fig. 4) is consistent with cyanobacterial activity, as observed in the field with a proliferation of cyanobacterial surface scums (personal observation), which are capable of atmospheric CO_2 uptake in eutrophic lakes (Gu and Alexander, 1996).

In the Madeira and Tapajòs rivers, a concentration increase in phytoplanktonic FA markers from HW to LW was recorded in the SPOM (Table 4). In the turbid waters of the Madeira, the lower flow velocity and turbulence in LW at its confluence with the Amazon may explain the increase in phytoplanktonic FAs; only one point was sampled, located close to the confluence with the Amazon, where currents from the Madeira are weak. In addition, it may lead to small blooms of phytoplankton, especially cyanobacteria, as described for similar riverine conditions (Mitrovic et al., 2003). In the Tapajòs River, increases in specific FA markers with a $\delta^{13}C$ enrichment from HW to LW (Fig. 4; Clear/Black rivers) clearly demonstrates that, as reported previously (Schmidt, 1982), the deep euphotic zone, the width of the river mouth and the slow current in the LW season, lead to bloom populations of phytoplankton and cyanobacteria.

As confirmed by FAs and stable isotope seasonal differences, cyanobacteria and C_3 aquatic plant can be considered as major contributors to both nitrogen and carbon cycling in the Amazon Várzea, particularly during the LW.

4.3. Connectivity between Várzea and the Amazon River

In the Amazon basin, hydrological conditions of rivers and lakes render the Várzea strictly dependent on water level fluctuation in the main river throughout perennial channels (Irion et al., 1997). Therefore, the connectivity between Várzea and rivers leads to seasonal transfer of OM (Moreira-Turcq et al., unpublished results). Lower concentrations of FA markers in HW SPOM from Várzea and rivers were due to the flood dilution (Table A5–A7, Appendix; Fig. 3). Indeed, during HW, the Várzea were totally connected to the mainstem as a result of the river flood, as in Curuaï Várzea, where water and suspended solid storage in the floodplain were controlled from November (lowest water level) to June (HW) by the Amazon mainstem and local precipitation (Bourgoin et al., 2007; Bonnet et al., 2008).

As in the Várzea, an increase in phytoplanktonic FA markers, including those from cyanobacteria, as well as aquatic plant FAs, was recorded from HW to LW in the Amazon River (Fig. 3; Table 4). In the mainstem, local phytoplanktonic growth is limited throughout the seasons due to a shallow euphotic depth, deep water column and intense vertical mixing (Sioli, 1984). An input of phytoplankton from the two main tributaries of the Amazon (the Negro and Solimões rivers) was trivial, as primary production does not occur in these rivers (Fisher, 1979; Hedges et al., 1994). This was confirmed in the present study in term of FA composition, with the low contribution of the cyanobacteria FA marker in the SPOM of Negro and Solimões rivers (Table 4). Thus, a low

contribution from these tributaries during LW, suggests a transfer of OM partly derived from phytoplankton, from the Várzea to the mainstem as the level of water (i.e. lowest water level occurred one month later), still allowed minimum connectivity between the Várzea and the main channel.

The increase from HW to LW in aquatic plant derived FAs (18:3ω3 and 18:2ω6) in rivers (Table 4) could be attributed, as for the Várzea, to the accumulation of detritus following the loss of plant biomass from the ecosystem. This increase was also recorded in the Solimões and Negro rivers (Table 4), which may be attributed to the contribution of aquatic plant detritus from upstream lakes and channels (Engle et al., 2008). However, a phytoplanktonic FA increase in contribution was not recorded in these two rivers (Table 4), which may result from a rapid degradation of this specific FA (Rontani, 1998).

Acknowledgements

This research is a contribution to the CARBAMA project, supported by the ANR (French National Agency for Research), and conducted within an international cooperation agreement between the CNPq (National Council for Scientific and Technological Development – Brazil) and the IRD (Institute for Research and Development – France). We thank Professor G. Boaventura from the University of Brasilia and Dr P. Seyler from the IRD for administrative facilities. We are also grateful to the two anonymous reviewers for help and constructive reviews.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.orggeochem.2011.08.011.

Associate Editor—**T.S. Bianchi**

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