

CH₄ and CO₂ from Decomposition of *Salvinia auriculata* Aublet, a Macrophyte with High Invasive Potential

Irineu Bianchini Jr.^{1,2} · Marcela Bianchessi da Cunha-Santino^{1,2}

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Abstract Tropical floodplain wetlands are favorable environments for the growth of aquatic macrophytes and palustrine plants. Such plants and phytoplankton are usually the key sources of autochthonous detritus within floodplain lakes. An experiment was conducted in order to compare the production of methane (CH₄) and carbon dioxide (CO₂) from anaerobic decomposition of *Salvinia auriculata*. The incubations were prepared and maintained (138 d) at 4 different temperatures (15.3, 20.8, 25.7 and 30.3 °C), and the daily rates of CH₄ and CO₂ were measured by gas chromatography. Periodically, the dissolved organic carbon, electrical conductivity, pH and redox potential were also measured. The anaerobic mineralization of *S. auriculata* was a sensitive process with respect to temperature, and CH₄ was the minor product (CH₄ yield: 0 to 5.1 % of C-emissions). The Q₁₀ calculated for mineralization was 1.16, and, after 138d, the CO₂ yields were closed (average: 23.6 %). The CH₄ was a secondary end product of *S. auriculata* mineralization, making CO₂ the main greenhouse gas produced from this source. The increase in temperature should favor the formation of CH₄ and shorten the time required for their formation. However, due to the

large difference between the yields, CO₂ should remain the main end product of decomposition.

Keywords Aquatic plants · Decomposition · Greenhouse gas · Floodplain lake

Introduction

Floodplain wetlands are hydrodynamically governed by the flood pulses produced by the rising river water level and consequent lateral overflow. Cyclic floods are a key factor controlling the metabolism (primary production rates, gas emissions, and biogeochemical cycles) and structure of the floodplain systems (Junk et al. 1989; Bloom et al. 2012). Landforms in tropical meandering floodplain rivers enclose shallow lakes representing favorable environments for the settlement of aquatic macrophyte communities and palustrine plants (Van Geest et al. 2005). Blooms of aquatic macrophytes with high growth coefficients usually occur in natural (i.e., lakes and wetlands) and man-made tropical freshwater ecosystems. Frequently, the occurrence of *Egeria* spp (common waterweed), *Eichhornia crassipes* (water hyacinth), *Oxycaryum cubense* (sedge), *Pistia stratiotes* (water lettuce), *Salvinia* spp (e.g., giant salvinia) and *Typha domingensis* (southern cattail) are observed in tropical regions (Bini et al. 1999; Tanaka et al. 2002; Thomaz et al. 2006; Martins et al. 2008; Bianchini Jr. and Cunha-Santino 2014). The interaction of hydrology, high temperatures and massive primary production classify tropical floodplain wetlands among the most productive natural environments providing large amounts of detritus to these systems (Merritt and Lawson 1992; Neiff et al. 2006). At floodplains where summer

✉ Irineu Bianchini, Jr.
irineu@ufscar.br

Marcela Bianchessi da Cunha-Santino
cunha_santino@ufscar.br

¹ Departamento de Hidrobiologia, Universidade Federal de São Carlos (UFSCar), Rodovia Washington Luiz, km 235, São Carlos, SP, Brazil CEP: 13565-905

² Programa de Pós-Graduação em Ecologia e Recursos Naturais, UFSCar, Rodovia Washington Luiz, km 235, São Carlos, SP, Brazil CEP: 13565-905

coincides with the rainy season, occurs two converging events to increase the production and emission of methane, and anaerobic cycling of organic detritus: the increase of temperature and the generation of anaerobic soils due to rain and overflow of rivers (Gedney et al. 2004; Melack et al. 2004; Bloom et al. 2012). Considering all ecological functions and multiple uses provided by floodplain wetlands, these environments are among the most threatened ecosystems (Junk and Wantzen 2004; Junk et al. 2013).

Palustrine plants, aquatic macrophyte and phytoplankton represent the main sources of autochthonous detritus within tropical floodplain wetlands. Detritus input loading functions can significantly alter wetland carbon and nutrient dynamics by changing the quantity and quality of plant litter inputs (Duke et al. 2015). Soils heavily loaded with organic matter emit significantly more carbon dioxide (CO₂) than those that have received little or no organic matter (Winton and Richardson 2015). In the early phases of decomposition, the formation of dissolved organic carbon came from leaching of senescent plants (Hanamachi et al. 2008). The lignocellulosic fibers (i.e., particulate organic matter) of macrophyte are a substantial source of refractory carbon. Owing to high rates of primary production in tropical wetlands, aquatic plant detritus accumulates massively on sediment making it a key source of methane (CH₄) and CO₂ emissions in floodplain lagoons. Tropical systems may account for 60 % of global atmospheric CH₄ emissions (Wang et al. 1996). As well as the detritus degradability (i.e., labile carbon or refractory carbon), other regulatory variables (e.g., pH, temperature, salinity, presence of oxygen and oxidized compounds and nutrient availability) act on methanogenesis, a terminal step during biodegradation of organic matter in anoxic layers of sediments (Magonigal et al. 2004). Considering the high production of detritus from aquatic macrophyte in tropical wetlands and the importance of environmental variables in the CH₄ production, we conducted an experiment to compare the production of methane and carbon dioxide from decomposition of *Salvinia auriculata*, a macrophyte species with a high occurrence in tropical aquatic systems and with high invasive potential (Pott and Pott 2000). We hypothesized that in similar physico-chemical conditions (e.g., pH, availability of nutrients, redox potential, dissolved organic carbon), during the anaerobic decomposition of *Salvinia auriculata*, the CH₄ proportion of daily rates of emission, as well as the CH₄ and CO₂ yields are guided by the temperature. Thus, this experiment addresses the anaerobic decomposition of frequent aquatic macrophyte species in relatively warm environments (e.g., anaerobic sediments and waterlogged soils).

Methods

Study Area

The Óleo Lagoon is an oxbow lagoon within the floodplain of the Mogi-Guaçu River located in the Jataí Ecological Station (21°33' to 21°37'S and 47°45' to 47°51'W) in São Paulo State, Brazil. This is a small, shallow (area=19,470 m² and Z_{mean} 2.55 m) and low volume (49,613 m³) lagoon (Petraço 2006). The dissolved oxygen availability in the bottom of the water column is low (0.1–1.6 mg L⁻¹) and the sediments present high amounts (19–33 %) of organic matter (Sciessere 2011). The high macrophyte colonization in the littoral zone (Sciessere et al. 2011) includes *Salvinia auriculata* that represent an autochthonous detritus source in this lagoon (Cunha-Santino and Bianchini Jr. 2008). The climate is characterized by a rainy season with temperatures of up to 28 °C (November to April) and a dry season with temperatures below 21 °C (May to October). The mean annual precipitation is 1,550 mm and the mean annual temperature is 21.7 °C (Ballester and Santos 2001).

Salvinia genus (floating fern) occurs in aquatic environments of many tropical regions, being absent in cold regions (Boschilia et al. 2006). These floating macrophytes stand out because they have skills to quickly colonize many aquatic environments, being comparable to the water hyacinth (Mitchell and Tur 1975). Excessive growth of these species is due to high growth rates and reproductive capacity, mainly vegetative form (Fernández et al. 1990), associated with environmental changes that increase the availability of nutrients in water bodies and create favorable conditions for its development (Gopal 1990). Although the high growth rates of these plants are usually associated with high concentrations of nutrients (Thomas et al. 1999), there are records of large stands of *Salvinia* even in oligotrophic environments (Camargo and Esteves 1995). At the sites where there is *Salvinia* incidence it is common to observe high biomass values (e.g., the average value range (dry weight basis): 12.5 to 27.2 kg m⁻²; Lolis 2008). *Salvinia auriculata* (= *S. molesta*) is a native specimen in Central America and South America, as well the other species of *Salvinia* genus present very high occurrence in Neotropic region; and there are reports of *S. molesta* occurrence in the United States of America (Jacono et al. 2001).

Material Sampling and Decomposition Assays

Individuals of *Salvinia auriculata* Aublet (a free-floating aquatic fern) were harvested in the littoral region of the Óleo Lagoon. In the laboratory, the plant samples were washed with deionized water and oven dried (50 °C) until constant dry mass (DM). One day prior to the assay setup, water samples were collected in the Óleo Lagoon at three distinct depths (surface=0.1 m, middle=2.5 m and bottom=5.0 m) using

the Van Dorn bottle. The samples were mixed and filtered (cellulose acetate membrane, Millipore 0.45 μm pore size) to remove large organisms and coarse detritus. To measure the concentration of carbon dioxide and methane resulting from the anaerobic decomposition, incubation chambers ($n=4$) were prepared with 8 g of *S. auriculata* DM tissues per L of filtered water sample and 10 ml of an indigenous inoculum from interstitial Óleo Lagoon sediment water. These assays were setup using a 1-L Boeco glass laboratory bottle with a screw cap and pouring ring. The elemental analysis of carbon in *S. auriculata* tissue (35.89 %) was made using a CHN Analyser - Carlo Erba EA1110. The chambers were set up with airtight caps equipped with two glass tubes connected by small rubber septa. Four control incubations were also prepared with water and indigenous inoculum from the Óleo Lagoon. In order to establish a reduced medium inside the decomposition chambers, N_2 was bubbled into each chamber for 20 min prior to the startup of the experiment. Anaerobiosis of the medium was established within the first hours of incubation (Cunha-Santino and Bianchini Jr. 2013). Based on the kinetics of dissolved oxygen uptake (oxygen consumption coefficient: 0.040 d^{-1} and maximum oxygen consumption concentration: 244 mg DO g^{-1} detritus) during the degradation of *S. auriculata* detritus (Bianchini Jr. et al. 2011), on the initial saturation concentration of dissolved oxygen decomposition in each chamber (at 15.3 °C, 10.08 mg L^{-1} ; 20.8 °C, 9.09 mg L^{-1} ; 25.7 °C, 8.26 mg L^{-1} ; and 30.3 °C, 7.56 mg L^{-1}) and on the initial detritus mass used to measure CO_2 and CH_4 (ca. 8 g), all the chambers' medium became anaerobic after 2 h 30 min from adding *S. auricularia* tissues to each chamber. The chambers were incubated in the dark at controlled temperatures ($\sim 15, 20, 25,$ and 30 °C) for 138 days. Thermistors were used three times per week to check the incubation temperature, with mean temperatures of 15.3, 20.8, 25.7, and 30.3 °C. The temperature collection was selected to include the most common range (i.e., average: 18.7 ± 2.2 °C to 28.1 ± 1.5 °C), and also including any extremes temperatures (Tmin: 15.8 °C; Tmax: 29.5 °C); Cunha-Santino and Bianchini Jr. (2008).

Periodically, three subsamples (10 μl) of headspace gases (total volume of headspace = 150 ml) in the incubation chambers (volume = 1 L) were collected using a needle gas pump (volume = 1.0 ml) and the concentrations of CO_2 and CH_4 were quantified ($n=102$) by gas chromatography (GC chromatograph, model 370 column, Porapak N; carrier gas, H_2 flow of 31.5 ml min^{-1}). The concentrations of these gases were compared to standard curves previously prepared with CO_2 (purity, 99.998 %, $r^2=0.98$, $n=10$) and CH_4 (purity, 99.99 %, $r^2=0.99$, $n=10$). After each measurement, the incubations were depressurized to atmospheric pressure by injecting gaseous nitrogen. This procedure was adopted to reset the daily C-gas (C-gas = C- CH_4 + C- CO_2) formation and also to maintain the medium free from oxygen

contamination. Over 137 days (sampling days: 0, 2, 4, 10, 13, 22, 29, 43, 60, 84, 114, and 137), additional decomposition chambers following the same proportion of gas sampling chambers (8 g L^{-1}) were set up to measure dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), hydrogenionic potential (pH), electrical conductivity (EC) and redox potential (Eh). DOC and DIC were measured ($n=3$) in the dissolved fraction by Pt-catalyzed nondispersive combustion and detection in infrared gas analysis in the Shimadzu TOC-5000A analyzer. The DOC concentrations were compared to a potassium hydrogen phthalate-based standard curve. The Eh and pH were measured using a potentiometer (Digimed DMPH-2) and the EC with a conductivity meter (Digimed DM3).

Mathematical Modeling and Statistical Analysis

Considering the CO_2 and CH_4 formations, resulting from anaerobic decomposition of *S. auriculata*, and the carbon mass balance in the incubations, the mineralization coefficients were computed, considering this process as first-order kinetics (Eq. 1; Debusk and Reddy 2005). Thus, the half-life ($t_{1/2}$) was calculated by Eq. 2. The daily concentrations of CH_4 and CO_2 were accumulated over time in order to evaluate the CO_2 and CH_4 yields.

$$k = \frac{\ln(w_t/w_0)}{t}, \quad (1)$$

$$t_{1/2} = \frac{\ln(0.5)}{-k}, \quad (2)$$

where: k = mineralization rate constant at temperature of interest (d^{-1}); w_t = remaining particulate organic carbon after 138 days + DOC mass; w_0 = initial mass of detritus (on carbon basis; i.e., $8 \text{ g} \times 0.3589$); t = elapsed time of the experiment (138 d).

The Q_{10} values were obtained from the relations (exponential) between the temperature and mineralization coefficient and between the temperature and maximum quantity of CH_4 produced (Bowie et al. 1985). The mineralization coefficients were considered as temperature dependent (Kätterer et al. 1998).

DOC concentrations and values of EC, Eh and pH were submitted to Canonical Discriminant Analysis (Box test (chi-square asymptotic approximation); Box test (Fisher F asymptotic approach); Kullback test; Wilks Lambda test (Rao approach); Pillai's trace test; Hotelling-Lawley's trace test; Roy's largest Root test) to check differences among the incubations at different temperatures. The significance level (α) was 0.05, and the H_0 (null hypothesis; i.e., there were no differences among the incubations) was rejected when p -values were smaller than α . The Multivariate Analysis was performed using XLSTAT Version 2008.3.01 software.

The normality of CH₄ and CO₂ production and the ratio C-CH₄:C-gas (C-gas=CH₄+CO₂) data were evaluated using the Shapiro-Wilk test. If normality was achieved, the ANOVA test with repeated measures was conducted. Otherwise, the Kruskal-Wallis test was applied followed by the Dunn multiple comparison test. Differences were considered significant where $p < 0.05$. The statistical analyses were performed using the PAST software, version 2.16 (Hammer et al. 2001).

Results

Except the Box tests (chi-square $p = 0.057$; Fisher asymptotic approximation of F $p = 0.061$) and Kullback test ($p = 0.0687$), the other tests (Wilks Lambda test $p = 0.000$; Pillai's trace $p = 0.003$; Hotelling-Lawley's trace test $p < 0.0001$; Roy's largest Root test $p < 0.0001$) rejected the null hypothesis (i.e., the conditions between incubations were different p values $< \alpha$). Eh and pH were the variables responsible for this discrimination, the others (DOC and EC) did not differ significantly between the incubation bottles at different temperatures. According to these variables, multivariate analysis point out that only incubations at 15 °C were different, and the others were similar among them. Regardless of the temperature of incubation, the pH varied between 5.84 and 7.42; the Eh values ranged between 105 and -259 mv; the EC presented variations between 17 and 1508 $\mu\text{S cm}^{-1}$ and DOC between 1.6 and 198.5 mg L^{-1} (Table 1). Except for Eh, the minimum values presented in Table 1 refer to the water sample of the Óleo Lagoon used in the decomposition chambers. The DOC concentrations corresponded to ca. 1 to 6 % of the total amount of C added to the incubations (ca. 2,871 mg).

The C-gas daily rates Fig. 1, as well as C-CH₄ daily rates were affected by the temperature. The C-gas daily rates were higher in incubations with increasing temperatures. Consequently, both mineralization and gas yields were higher in the incubations maintained at higher temperatures (Table 2). The half-life of *S. auriculata* anaerobic mineralization varied between 257 (25.7 and 30.3 °C) and 317 d (15.3 °C). The C-gas production was similar at 15.3 and 20.8 °C ($p > 0.05$) and between 25.7 and 30.3 °C ($p < 0.001$). The coefficients of variation (mean values) of the daily rates among incubations were 29 % for CO₂ and 38 % for CH₄, considering all temperatures.

Only at 15.3 °C was the methane not produced (Fig. 2). In general, the higher the temperature, the faster the beginning of methane production was. The proportion of methane in the daily rates also tended to be higher in the incubations with higher temperatures. The C-CH₄:C-gas varied between 0.56 (20.8 °C) and 0.62 (30.3 °C) and the C-CH₄:C-gas proportions were similar ($p > 0.05$). The initial time of methane production varied between 26 (25.7 °C) and 32 days (20.8 °C) and the

Table 1 Average, standard deviation (SD), minimum (Min.) and maximum (Max.) values of pH, redox potential (Eh), dissolved organic carbon (DOC), and electrical conductivity (EC) during anaerobic decomposition of *Salvinia auriculata*, under 4 different temperatures

	Average	SD	Min.	Max.
pH				
15.3 °C	6.87	0.5	5.84	7.42
20.8 °C	6.73	0.4	5.84	7.18
25.7 °C	6.71	0.3	5.84	7.04
30.3 °C	6.71	0.3	5.84	7.13
DOC (mg L ⁻¹)				
15.3 °C	67.36	28.6	1.6	108.1
20.8 °C	86.1	52.2	1.6	166.2
25.7 °C	90.1	59.3	1.6	198.5
30.3 °C	85.4	58.2	1.6	191.6
Eh (mV)				
15.3 °C	-89	101	-192	105
20.8 °C	-122	91	-213	61
25.7 °C	-145	85	-216	39
30.3 °C	-174	71	-259	9
EC ($\mu\text{S cm}^{-1}$)				
15.3 °C	881	347	17	1242
20.8 °C	990	405	17	1467
25.7 °C	1079	406	17	1508
30.3 °C	1063	381	17	1396

yield of this gas increased with increasing temperatures ($Q_{10} = 1.56$). The CH₄ yields were always smaller than the CO₂ yields. The anaerobic mineralization of *S. auriculata* is a sensitive process regarding temperature, with a predominant production of CO₂ (CO₂ yield: 82 to 100 % of C-emissions). The Q_{10} calculated from the mineralization rates constant (k) was 1.16, and after 138d, the CO₂ yields were closed (22.3 % at 20.8 °C and 24.8 % at 25.7 °C); Table 2.

Discussion

In floodplain lakes, the difference of magnitude between the growth rate constants (average: doubling time ca. 7 d; Bianchini Jr. et al. 2015) and decomposition rate constants (half-life between ca. 17 and 280 d; Webster and Benfield 1986) of macrophytes affects the dynamics and metabolism of the environment. Often in these environments, most detritus produced in littoral regions derives from macrophyte contributing to the organic matter storage, sediment diagenesis and biogenic gas emissions, such as CH₄, CO₂, N₂, H₂S (Reddy and DeLaune 2008). Among the regulatory variables of biogenic emissions in these environments, the type of detritus (i.e., macrophyte species) and its structure (i.e., fibers, leachate, roots, rhizomes, and leaves) are usually mentioned

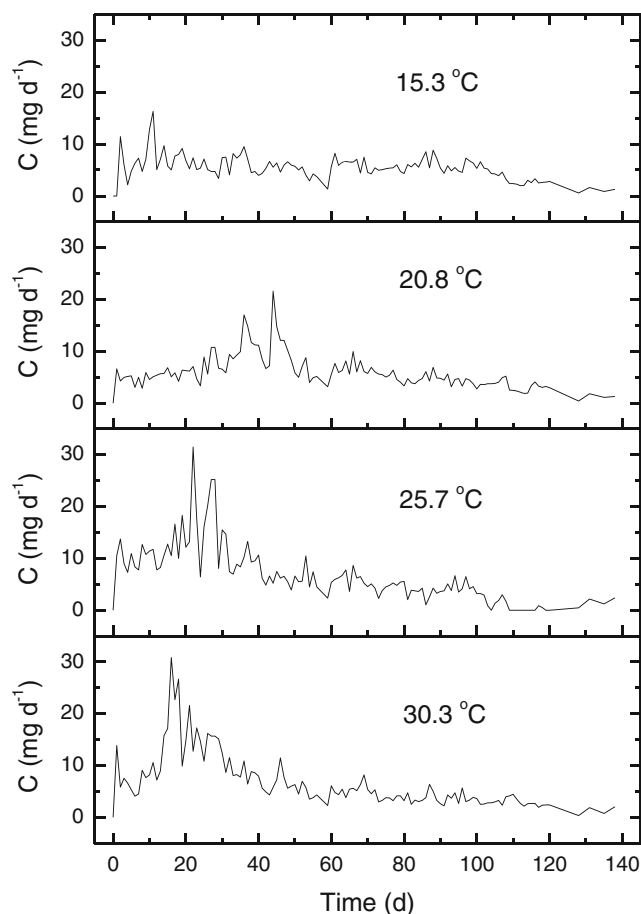


Fig. 1 Temporal changes in the daily rates of C-gas emission (Σ CO₂, CH₄; on carbon basis) from anaerobic decomposition of *Salvinia auriculata*, under different temperatures (15.3, 20.8, 25.7, and 30.3 °C). Coefficient of variation of the daily rates (mean values): 29 % for CO₂ and 38 % for CH₄

(Bianchini Jr. et al. 2010; O’Sullivan et al. 2010). The present study showed that anaerobic mineralization of *S. auriculata* was a temperature sensitive process. The increase in the temperature shortened the half-life time of detritus and increased the CH₄ yield. In addition, the increase in the temperature decreased the time required to start methane formation. In turn, the CO₂ yields were always higher than the CH₄ yields and the temperature varied slightly.

Taking into account the intrinsic factors, the detritus nutritional composition affects decomposition pathways (Parsons

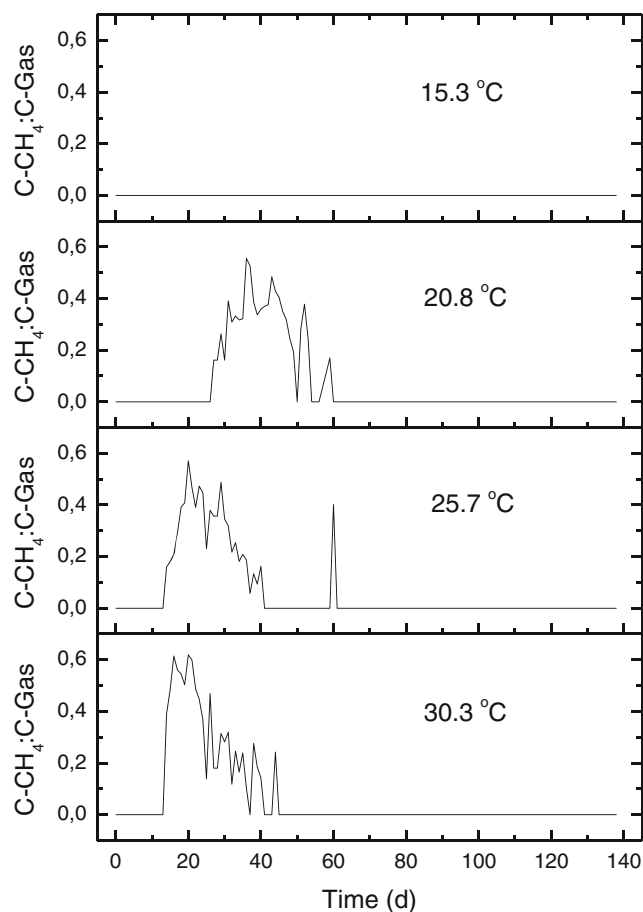


Fig. 2 Ratio of C-CH₄ in the daily rates of C-gas emissions from anaerobic decomposition of *Salvinia auriculata*, under different temperatures (15.3, 20.8, 25.7, and 30.3 °C)

et al. 2014), in this case promoting CH₄ formation. As for anaerobic decomposition of roots, rhizomes and *Scirpus cubense* (sedge) leaves, heterotrophic organisms showed heavy root consumption whereas rhizomes were the most refractory detritus. In addition, detritus with higher ash content was found to show higher CH₄ production (Romeiro and Bianchini Jr. 2006). Besides the nutrient content of the detritus as a supplement in methane formation, anaerobic degradation of *Utricularia breviscapa* (bladderwort) showed strong evidence that the CH₄ formation was associated to cellulase activity (Cunha-Santino and Bianchini Jr. 2007) and, therefore,

Table 2 Carbon budget from the anaerobic decomposition of *Salvinia auriculata* under 4 different temperatures, after 138 days

	MC (%)	DIC (%)	C-Gas (%)	C-CH ₄ (%)	C-CO ₂ (%)	k (d ⁻¹)	t _{1/2} (d)
15.3 °C	26.1	2.5	23.5	0.0	23.5	0.0022	317
20.8 °C	28.0	2.5	25.5	3.3	22.3	0.0024	291
25.7 °C	31.1	2.1	28.9	4.1	24.8	0.0027	257
30.3 °C	30.9	2.2	28.7	5.1	23.6	0.0027	259

Where: MC mineralized carbon; DIC dissolved inorganic carbon; C-Gas yield of gas formation (Σ C-CO₂, C-CH₄; on carbon basis); C-CH₄ yield of methane formation (on carbon basis); C-CO₂ yield of CO₂ formation (on carbon basis); k mineralization rate constant; t_{1/2} half-life time

dependent on anaerobic degradation of cellulose (El-Shinnawi et al. 1989; Leschine 1995).

Specific requirements of methanogenic archaea, in agreement with our results (i.e., null CH₄ emission rates), enabled us to assume that in the Óleo Lagoon (and other similar aquatic systems) that CH₄ formation during decomposition of aquatic macrophytes depends overwhelmingly on the input of aquatic macrophyte detritus, i.e., the temporal intensity variation. In the present case, asynchronies were observed between the predominance of the detritus input (autumn - winter) from the higher values of CH₄ emission and denitrification (spring - summer) (Gianotti and Santos 2000; Ballester and Santos 2001). However, during the senescence period, the macrophytes contributed strongly to the detritus input. Notably in this floodplain, the cycling of autochthonous detritus plays a main role since the flooding currently is unusual owing to the current predominance of low flow of Mogi Guaçu River (the last river overflow was in 1999), and to the deepening of the river channel due to sand mining in the upstream section (Fushita and Santos 2015).

Although the CH₄ is predominant in the daily emission rates, these episodes occurred in short periods. Probably this event elapsed from the selected temperatures (Gerardi 2003), however the temperatures from our experiment cover the changes that occur in tropical aquatic systems. Considering only the yields, the methane production (3.3–5.1 %) suggests that this process is independent from aquatic macrophyte (i.e., submerged and emerged species) during decomposition. Yields of CH₄ formation at ca. 20 °C during degradation of both submerged (0.4–23.3 %) and emerged (2.3–27.1 %) macrophyte were similar (Bianchini Jr. et al. 2010). The CH₄ yields suggest that, besides the chemical composition of the detritus (i.e., nutrients' content, labile and refractory organic fractions), the temperature also interferes in the CH₄ formation. An in vitro experiment showed that CH₄ formation was inhibited by a pH decrease due to intense CO₂ formation during the beginning of *Cabomba furcata* (fanwort) degradation (Cunha-Santino et al. 2006). The values of pH, Eh, DOC, and EC, registered during anaerobic decomposition of *S. auriculata*, indicated that the physical and chemical medium for the decomposition were not similar in all incubations, and may have induced changes in mineralization routes.

As commonly observed, temperature was a key factor in CH₄ formation (Nozhevnikova et al. 1997) and also in anaerobic mineralization of aquatic macrophytes (Cunha-Santino and Bianchini Jr. 2013). Comparing the results, methanogenesis was more sensitive to temperature changes than gross anaerobic mineralization. The Q₁₀ value for CH₄ production is slightly lower than the normally usual value registered; a compilation of temperature-response studies using wetland soils report an average Q₁₀ of 4.1 for CH₄ production (Segers 1998). The lowest value of Q₁₀ might result from the chemical composition of *S. auriculata* tissues

prior to the incubation (Erhagen et al. 2013). Although the metabolic routes that culminate in CO₂ were always predominant; methanogenesis rather than CO₂ formation was favored by increasing temperatures. This variable anticipated the time required to start methanogenesis. Another factor that explains the time required for CH₄ production is the consumption of alternative electron acceptors (i.e., denitrification, Fe(III)-reduction and sulfate reduction); in this case, these processes can also be anticipated by the increase in temperature (Meganigal et al. 2004). Even though methane is a by-product of anaerobic decomposition of aquatic plants, the expected increase in temperature (IPCC 2013) should favor the formation of this gas and retract the time required for their formation, as usually registered for tropical wetlands (Bloom et al. 2012). However, due to the large difference between the yields, CO₂ should remain as the main end product of decomposition. In conclusion, the growing current rise of temperature is a factor to be concerned about that will strongly influence the process related to final carbon degradation products. In the case of the oxbow lakes of the Mogi-Guaçu floodplain, with reference to the Óleo Lagoon (a tropical horseshoe lake), the CH₄ was a secondary end product of *S. auriculata* mineralization, and CO₂ was the main greenhouse gas produced from this autochthonous source of carbon.

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