

Temporal and Spatial Patterns in Inputs and Stock of Organic Matter in Savannah Streams of Central Brazil

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ABSTRACT

Coarse particulate organic matter (CPOM) inputs from riparian vegetation into streams and CPOM benthic stock vary naturally in space and time, but most studies in the tropical savannah (Cerrado) have been done over a small temporal scale (<1 year), which does not allow for the determination of inter-annual patterns. We found that CPOM collected over two years differed temporally and spatially, whereas there was no significant variation between years for the benthic stock, which indicates high stability in the energy balance of streams. The largest monthly inputs occurred between August and October, at the end of the dry season and the onset of the rainy season, which was partially explained by precipitation. Other factors such as photoperiod, which was not studied, could also have important

roles in this pattern. Spatial differences in CPOM between streams were attributed to topography and channel morphology. The plant density was lowest in the stream with a more irregular topography and a deeper channel, which results in drier riparian soil. The benthic stock was highest in the stream with a flat channel, where the lower water speed facilitates the accumulation of CPOM in the stream bed. Inter-annual differences in CPOM were attributed more to the differences in the beginning of the dry and wet periods between years than to the average values of precipitation. Longer-term studies are needed to clarify this temporal pattern.

Key words: tropical; freshwater; riparian zone; headwaters; CPOM; Cerrado.

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INTRODUCTION

Riparian forests, formed by vegetation that follows streams and river channels, constitute the interface between terrestrial and aquatic ecosystems, and promote important ecological functions (Fischer and Fischenich 2000; Wantzen and others 2008; Chapin III and others 2011). They regulate exchanges between terrestrial and aquatic environ-

ments, preventing the eutrophication of water courses, soil erosion, and siltation (Naiman and others 2000; Smith and others 2008). The dense riparian gallery formed in association with small streams (Ribeiro and Walter 2008; Hart and others 2013) limits the photosynthetic process (Gücker and others 2009; Kiffney and Richardson 2010) and provides inputs of allochthonous coarse particulate organic matter (CPOM) into channels, which is thought to be a main source of energy in headwater streams (Naiman and others 2005; Wantzen and others 2008). Riparian forests also control the structure (richness and abundance) of aquatic communities (O'Driscoll and others 2006), as heterotrophic organisms in streams depend more on allochthonous CPOM than on that produced in the stream (Elosegi and Pozo 2005).

In the Brazilian savannah, riparian vegetation shows a high floristic diversity (Souza and others 2003; Silva Júnior 2004) due to its transitional character with the Amazonian forest, Caatinga, Pantanal, and Atlantic forest (Felfili and Silva Júnior 2005). The floristic composition of the riparian zone is also driven by regional climate (Carvalho and Uieda 2010), local edaphic characteristics (Silva Júnior 2001), discharge patterns, and sediment amount and characteristics (Steiger and Gurnell 2002). The soils of riparian zones usually have higher acidity, organic matter concentration, and moisture than the soil of Cerrado forests (Ribeiro and Walter 2008).

The amount of CPOM inputs into streams varies according to climate, vegetation type, the phenology of dominant species (Zhang and others 2014), the age of trees, and channel morphology, among other factors (Tank and others 2010; Lisboa and others 2015). CPOM inputs vary at different temporal and spatial scales (Colón-Gaud and others 2008; Kochi and others 2010). However, information about the influence of these scales on ecological processes in the riparian zones of tropical systems is scarce (Von Schiller and others 2008; Rezende and others 2014). In temperate systems, the CPOM inputs from riparian zones over the course of a year are well studied, but only recently have such inputs begun to be investigated in tropical regions (for example, Tank and others 2010; Gonçalves and others 2014). In temperate systems, these inputs are stimulated by decreases in temperature and light (Abelho 2001; Naiman and others 2005). However, in tropical systems, leaves fall throughout the entire year, but CPOM inputs increase in dry periods as result of water stress, to avoid desiccation (Gonçalves and others 2006; França and others 2009; Lisboa and others 2015;

Rezende and others 2016). However, there is no information on the inter-annual variability in these tropical systems, as most organic matter input studies have only been undertaken over one year (Nunes and Pinto 2007; Gonçalves and Callisto 2013; Lisboa and others 2015). There is also no information on the variation in CPOM inputs at a small spatial scale caused by local differences in vegetation, soils, or surface—groundwater exchange, as well as homogenous characteristics such as geology and climate (Ribeiro and Walter 2008).

Information on temporal and spatial variation in litter inputs are important to (i) assess the amount and residence time of CPOM in a system, (ii) establish reference conditions as a management tool, and (iii) plan the restoration of riparian zones (Naiman and others 2000; Heartsill Scalley and others 2012; Fonseca and Mendonça-Galvão 2014). Forecasting CPOM inputs can also allow for the development of dynamic models of CPOM at larger spatial and temporal scales (Ensign and Doyle 2006; Von Schiller and others 2008).

Therefore, our aim was to assess temporal (seasonal and inter-annual) and spatial variability in the CPOM inputs to three Brazilian savannah streams over two years. This study tested the following hypotheses: (i) the amount and composition of CPOM inputs vary in space and time because they are influenced by edaphic characteristics and vegetation type, and (ii) CPOM inputs vary from one year to another because they are affected by inter-annual patterns in rainfall.

MATERIALS AND METHODS

Study Site

The study was conducted in three third order streams according to the Strahler classification system (Strahler 1952): the Capetinga stream (CS) at the Ecological Station of Brasília University (ES UnB), the Cabeça-de-Veado stream (CVS) at the Ecological Station of the Botanical Garden of Brasília (ES JBB), and the Roncador stream (RS) at the Ecological Reserve of the Brazilian Institute of Geography and Statistics (ES IBGE), which together represent 45% of the Environmental Protection Area (EPA) of the Gama-Cabeça de Veado in the Federal District of Brazil. This area (Figure 1) is located in the Cerrado, a savannah in Brazil (15°52'–15°59'S and 47°50'–47°58'W), and has an elevation of between 1069 and 1089 m a.s.l. The climate in the Cerrado is tropical wet and dry, according to the Köppen classification (Aw), with a rainy season from October to

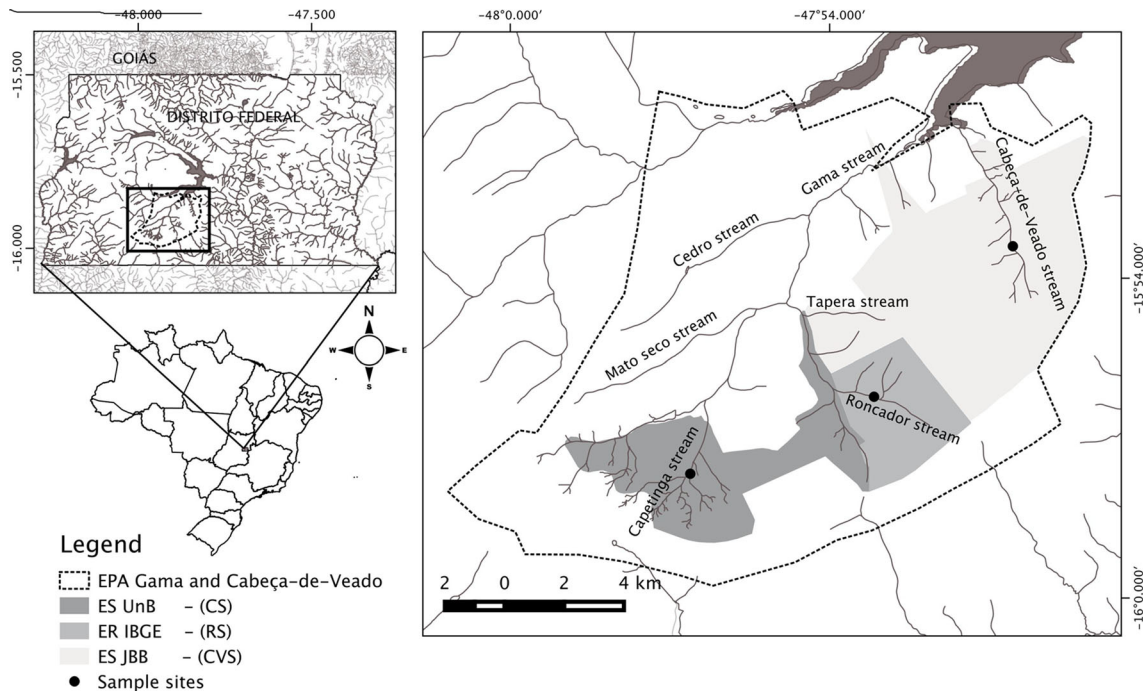


Figure 1. Location of the studied streams in the environmental preservation area (EPA): Gama-Cabeça-de-Veado in Cerrado of Central Brazil. ES UnB—Ecological Station of the University of Brasília—(CS) Capetinga Stream, IBGE—Ecological Reserve of the Brazilian Institute of Geography and Statistics—(RS) Roncador Stream and ES JBB—Ecological Station of Brasília Botanical Garden—(Cabeça-de-Veado Stream).

April (mean temperature $\approx 29^{\circ}\text{C}$) and a dry season from May to September (mean temperature $\approx 18^{\circ}\text{C}$). The mean annual precipitation is 1500 mm, ranging from 750 to 2000 mm (da Silva and others 2008). The most common soils in the Cerrado are latosols (46%), but in the riparian zone and flat areas, the predominant soil is hydromorphic fluvic, according to the Brazilian soil classification system (Reatto and Martins 2005; Vendrame and others 2010). The physiography of the hydrographic basins and the characteristics of the drainage area and water chemistry are described in Table 1.

The riparian zone is predominantly composed of natural vegetation with a height between 20 and 30 m and 70–95% canopy cover (Ribeiro and Walter 2008). The RS and CVS have a flat topography, being supplied by groundwater. The CS receives a groundwater supply, but over a smaller stretch, and has an irregular topography and a deep valley, which results in a drier riparian soil. Therefore, the areas studied contain species of plants such as *Protium heptaphyllum* (Aubl.) Marchand, *Psychotria carthagenensis* Jacq, *Schefflera morototoni* Maguire, Steyerm and Frodin, *Styrax camporum* Pohl, *Symplocos nitens* (Pohl) Benth, *Tapirira guianensis* Aubl., and *Virola sebifera* Aubl,

which can either be found in both well- and poorly drained soils at the same time or are adapted to specific conditions (either poorly drained or well-drained soils; Ribeiro and others 2001; Ribeiro and Walter 2008). The species richness of the vegetation is higher at the CVS (Nóbrega and others 2001) compared to the CS (Oliveira 2010), and the plant density is greater in the RS (Silva Júnior 2001).

Coarse Particulate Organic Matter Sampling

Coarse particulate organic matter (CPOM) was measured monthly at each study site over two years, from September 2010 to August 2012. The studied section of each stream was approximately 70 m, and the collection points were 15 m away from one another (Figure SM1—Supplementary Material). The sampling was performed to cover four components of CPOM: vertical input (VI), terrestrial input (TI), lateral input (LI), and benthic stock (BS). The VI, approximately 10 m from the edge of the stream, estimates the litter input from the canopy and is obtained using the plant material collected in three rows (~ 1 m distance between them) of six buckets (0.053 m^2 each; holes drilled in the base for rain water drainage) installed per-

Table 1. Description of Sampling Sites of Streams

Variables stream	Physio Geography of stream sub Basin		
	Capetinga	Cabeça-de-Veado	Roncador
Hydrographical basin	Paranoá/Paraná	Paranoá/Paraná	Paranoá/Paraná
Distance from source (km)	1.8	2.4	2.4
Altitude (m)	1089	1079	1069
Latitude (°)	15°57'43.68"S	15°53'22.15"S	15°56'14.77"S
Longitude	47°56'37.86"W	47°50'34.10"W	47°53'12.59"W
Buffer slope (°)*	8 ± 3	5 ± 1	5 ± 1
Order	Third	Third	Third
	Drainage area of sub basin stream*		
Total drainage area (ha)	581	1630	1227
Riparian vegetation (%)	7	5	9
Cerrado (%)	24	90	84
Cerrado field (%)	61	5	7
Agriculture (%)	3	0.5	0.5
Soil exposed (%)	5	0.01	0.2
Urban area (%)	0.3	0.06	0.4
	Abiotic variables of water stream		
Water temperature (°C)	18 ± 1	20 ± 0.9	19 ± 0.9
Water speed (m S ⁻¹)	0.7 ± 0.2	6 ± 2	0.5 ± 0.3
Dissolved oxygen (mg L ⁻¹)	7.5 ± 2	7.5 ± 3	5 ± 1
Electric conductivity (m S ⁻¹)	7 ± 4		10 ± 3
Water pH	7 ± 1	7 ± 0.8	6 ± 0.5
Water turbidity (NTU)	4 ± 2	3 ± 0.8	3 ± 0.8
Width (m)	3 ± 0.3	3 ± 0.5	2 ± 0.5
Stream depth (m S ⁻¹)	0.2 ± 0.2	0.3 ± 0.05	0.6 ± 2

*Data obtained by the geographic information system, GIS (2013), Laboratory of applied ecology of University of Brasília.

pendicularly to the channel and supported by synthetic ropes tied to trees. The TI estimates the CPOM falling directly to the ground (productivity of the riparian zone). It represents the potential stock that can be transported to the stream and contributes to the understanding of phenological patterns. The TI is obtained by collecting the plant material retained by two nets installed 1 m above the ground at each stream margin in the riparian zone (1 m²; 1 mm mesh size). The LI measures the indirect or linear CPOM input to the soil of the riparian zone that is moved downslope to the stream by gravity and the effect of runoff, wind, and animal action. To collect the organic material, two nets were installed (0.5 m²; 10 mm mesh size) at the ground level on both stream banks of each stream. The BS represents the CPOM accumulated on the stream channel bottom, which is directly influenced by water flow and the morphology of the streambed. Fifteen samples were collected (triplicate random samples from five points) from the stream bottom with a Surber[®] sampler (0.1024 m²; 0.25 mm mesh size).

In the lab, the LI and BS samples were washed to remove any inorganic material. All CPOM samples were dried in the oven at 60°C for 72 h (until a constant mass was reached) and separated into four categories: leaves, reproductive parts (flowers, seeds, and fruits) branches, and miscellaneous (including all remaining plant material). All fractions were weighed using a Sartorius Model 210A precision balance (Sartorius, Bel engineering). When the content of any sampler was lost due to the occurrence of a flash flood, as occurred with VI at the CS in January and March 2011 and January and February 2012, we assumed that it was not collected.

To calculate the CPOM input (vertical and terrestrial) and the benthic stock, the amount of organic matter mass collected from the traps was corrected by the exposure time and sampling area. The lateral CPOM input (L_i) was calculated by dividing two times the CPOM mass collected in a given lateral trap (M g⁻¹) by the width of the mouth of the trap (W_t m⁻¹) multiplied by the average width of the channel (W_c m⁻¹), which was

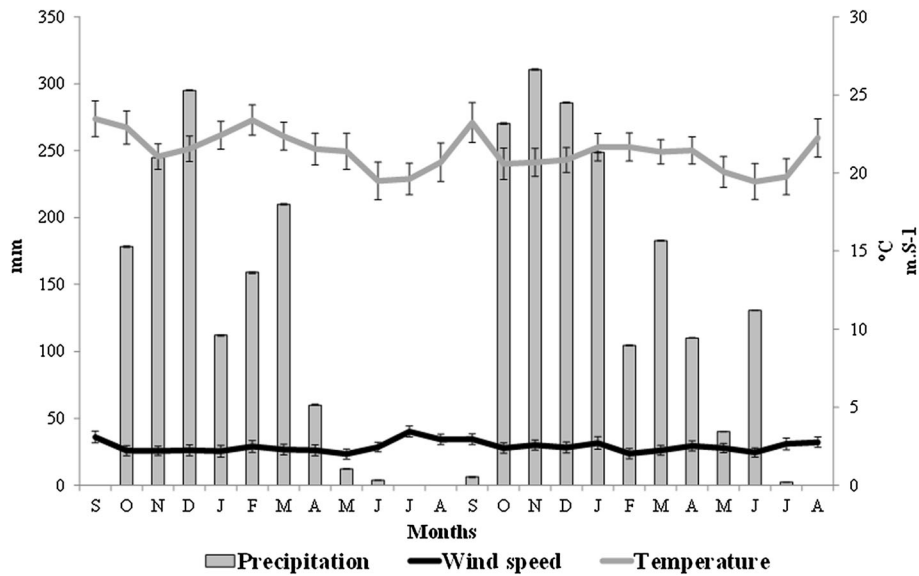


Figure 2. Monthly averages and standard error of wind speed (m S^{-1}) and temperature ($^{\circ}\text{C}$), and the total monthly rainfall (mm) during the study period (2010–2012).

then corrected by the number of days (T) of exposure to express the results per unit area of the river bed (g m^{-2} ; Elosegi and Pozo 2005; Pozo and others 2009; Kochi and others 2010) as follows:

$$L_i = \frac{2M}{W_t \times W_c} / T.$$

All average monthly input results were expressed per month, and the averages of the summed inputs and the benthic stock were expressed in g m^{-2} . The precipitation, wind speed, and temperature data (Figure 2) during the study period and the temporal series of precipitation data (1995–2014; Figure SM3) used to establish the seasonal precipitation patterns were provided by the Brasília Meteorological Station (2013).

Statistical Analysis

The normality of the CPOM data was assessed with the Kolmogorov–Smirnov test, the homogeneity of variances was assessed with Levene’s test, and values were $\ln(+1)$ -transformed if needed. The differences in the inputs of leaves, branches, miscellaneous, and reproductive parts (response variables) for the different CPOM components (VI, TI, HI, BS) among years, months, and their interactions (explanatory variable) were analyzed by a repeated-measures ANOVA (RM-ANOVA; Crawley 2007) using the collection apparatuses (buckets and nets) as repeated measurements. The different study sites were used as replicates that were repeated over months and years. Contrast analysis was used to discriminate differences between the categorical variables of years and months (Crawley

2007). RM-ANOVAs and contrast analyses were used to test for significant differences among the sampling sites (explanatory variable) in leaf, branch, miscellaneous, and reproductive part inputs (response variables) for different buckets and nets using the collection apparatuses (buckets and nets) as repeated measurements. The associations among the CPOM fractions (leaves, branches, miscellaneous, and reproductive parts) for different input and stock components and precipitation (rainfall), wind speed, and air temperature were assessed with Spearman’s correlation (Crawley 2007). We chose to use meteorological data from only one station because the variation in the precipitation recorded at the different stations distributed in the Federal District was only 7%.

RESULTS

Environmental Variables

During the study period, the annual precipitation was 1275 mm in the first year and 1562 mm in the second. The dry season was between May and September and the rainy season occurred between October and April. The highest monthly precipitation was 295 mm³ during the first year (December) and 310 mm in the second year (November; Figure 2). The lowest and highest mean monthly air temperatures were $19 \pm 4^{\circ}\text{C}$ and $24 \pm 4^{\circ}\text{C}$ (June and September), respectively, in the first year and $19 \pm 3^{\circ}\text{C}$ and $23 \pm 4^{\circ}\text{C}$ (May and September), respectively, in the second year. There was no difference between years in terms of temperature and wind speed (Figure 2).

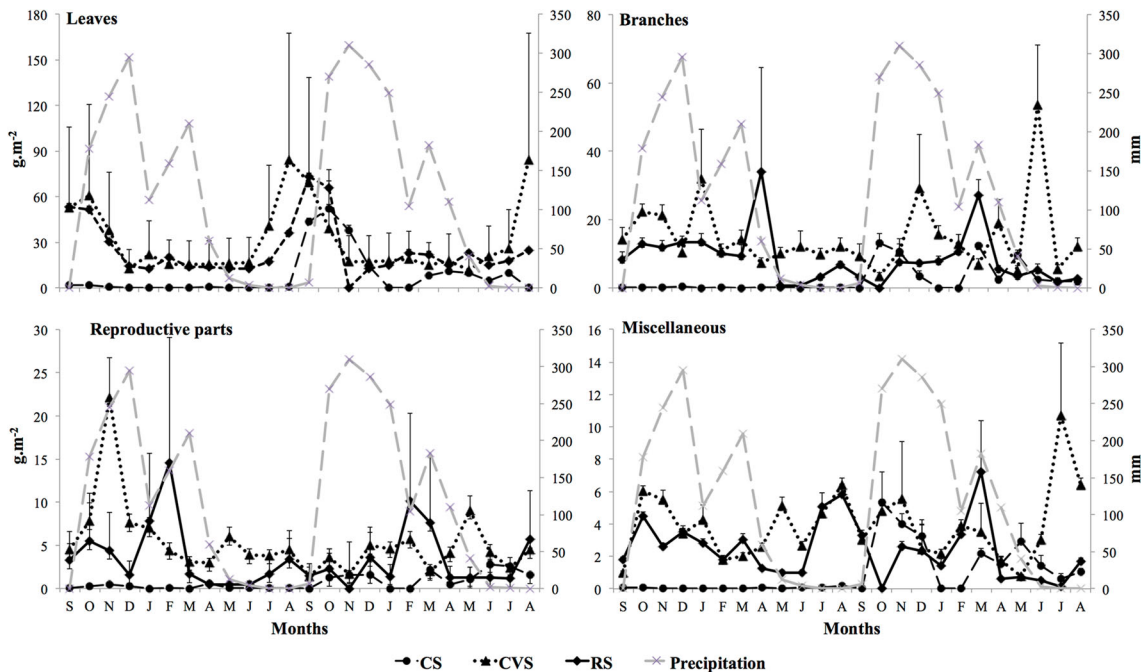


Figure 3. Mean and standard error of CPOM (g m^{-2}) fractions and monthly total precipitation (mm) among September 2010 and August 2012 into the vertical input at pristine streams in Cerrado of central Brazil.

Temporal Variation in Coarse Particulate Organic Matter Input and Benthic Stock

The average (\pm standard deviation) total CPOM input (VI, TI, LI) was $1624 \pm 30 \text{ g m}^{-2}$ (or 16.24 t ha^{-1}) in the first year and $3212 \pm 17 \text{ g m}^{-2}$ (or 32.12 t ha^{-1}) in the second year, and the average BS was $274 \pm 425 \text{ g m}^{-2}$ (or 2.74 t ha^{-1}) in the first year and $276 \pm 188 \text{ g m}^{-2}$ (or 2.76 t ha^{-1}) in the second year. There was a significant difference in CPOM input between years, with input being higher in the second year than in the first, while BS was similar in both years (Table SM1).

Over the 2 years of the study, of the total CPOM produced in the riparian zone, 59% was TI (from the ground of the riparian zone) and 41% was VI (fell directly into the stream). Of the total TI, only 18% of the CPOM entered the stream and 82% remained to accumulate in the soil of the riparian zone. Therefore, 51% of the CPOM produced in the riparian zone entered the stream in the first year and 60% of the TI accumulated in the soil, while 40% of the VI directly entered the stream in the second year. Of the total TI, only 2% entered the stream and 98% remained in the soil of the riparian zone.

The CPOM input was significantly correlated with rainfall for the LI ($r = 0.51$, $P = 0.01$) but not for VI ($r = 0.36$, $P = 0.12$), TI ($r = -0.19$, $P = 0.36$), or BS ($r = 0.28$, $P = 0.19$). However, within the CPOM

compartments, there were significant correlations between rainfall and some of the vegetation categories: in the VI with branches ($r = 0.42$, $P = 0.04$), in the TI with leaves ($r = 0.43$, $P = 0.05$) and reproductive parts ($r = 0.41$, $P = 0.04$), and in the LI with leaves ($r = 0.041$, $P = 0.04$) and reproductive parts ($r = 0.43$, $P = 0.05$). There were no correlations between CPOM input or benthic stock and wind speed or temperature. The variation in organic matter was explained by the factors of month, followed by month \times year, and finally by year, but more than 60% was unexplained (Residuals; Table SM1).

The largest monthly total CPOM input occurred between August (43.7 g m^{-2}) and October (44.3 g m^{-2}), which coincided with the transitional period between the end of the dry season and the beginning of the rainy season. The lowest values were obtained at the end of the rainy season (May; 15 g m^{-2}) and the beginning of the dry season (June; 12 g m^{-2}). November had the highest CPOM input during the rainy season (25 g m^{-2} month $^{-1}$). However, the average organic matter inputs were similar for the rainy ($748 \pm 10 \text{ g m}^{-2}$) and dry ($709 \pm 14 \text{ g m}^{-2}$) seasons. Leaves were the most abundant fraction in the composition of CPOM (62% of VI, 67% of TI, 61% of HI, and 50% of SB), and their contribution increased between August and October in all CPOM components (Figures 3, 4, 5, 6; Table SM1).

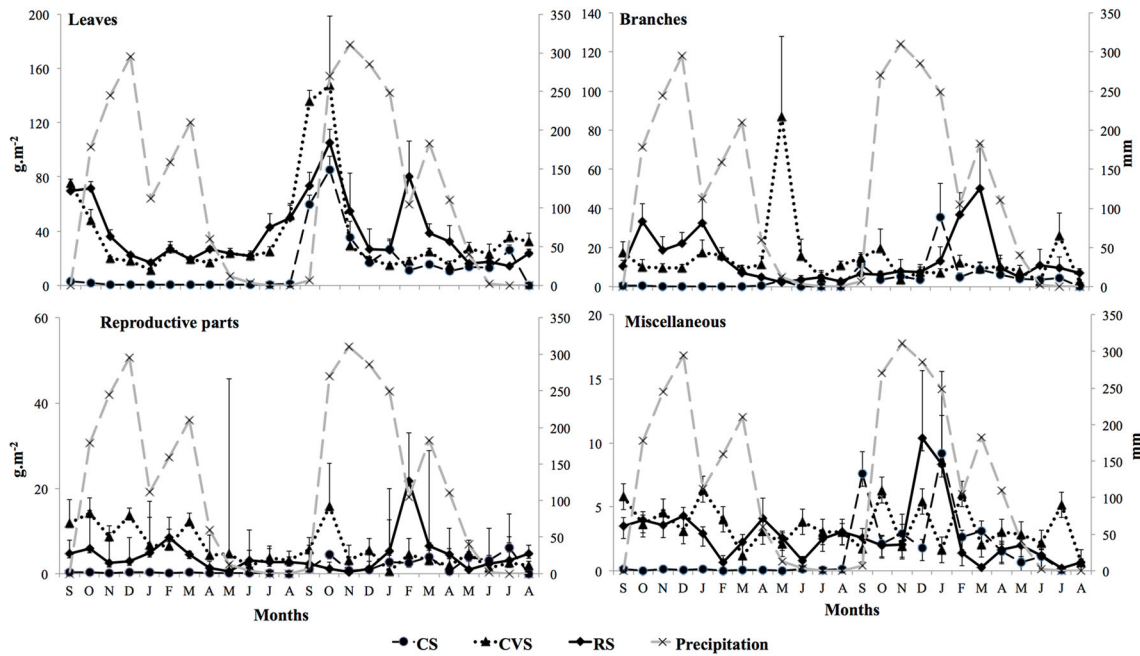


Figure 4. Mean and standard error of CPOM (g m^{-2}) fractions and monthly total precipitation (mm) among September 2010 and August 2012 into the terrestrial input at pristine streams in Cerrado of central Brazil.

Spatial Variation in Coarse Particulate Organic Matter Input and Benthic Stock

We found significant spatial differences in the average total CPOM input and benthic stock. The inputs and benthic stock also showed similar spatial patterns, with the former always being lower than the latter, although at varying degrees. The total CPOM inputs and benthic stock were higher at the RS ($1143 \pm 31 \text{ g m}^{-2}$ in the first year and $1330 \pm 43 \text{ g m}^{-2}$ in the second year and $3528 \pm 60 \text{ g m}^{-2}$ in the first year and $1818 \pm 72 \text{ g m}^{-2}$ in the second year, respectively), followed by the CVS ($314 \pm 31 \text{ g m}^{-2}$ in the first year and $1116 \pm 37 \text{ g m}^{-2}$ in the second year and $283 \pm 46 \text{ g m}^{-2}$ in the first year and $1237 \pm 56 \text{ g m}^{-2}$ in the second year, respectively) and the CS ($62 \pm 7 \text{ g m}^{-2}$ in the first year and $232 \pm 10 \text{ g m}^{-2}$ in the second year and $22.5 \pm 1.2 \text{ g m}^{-2}$ in the first year and $552 \pm 32.5 \text{ g m}^{-2}$ in the second year, respectively; Table SM2). The RS was statistically similar to the CVS in terms of vertical and terrestrial inputs, but these two were different from CS (Table SM3). At RS, the total benthic stock was higher than in the other streams (CVS and CS), but these differences were not significant for the leaf fraction alone (Figure 6; Table SM2).

DISCUSSION

The values of CPOM reported in this study were $1624 \pm 30 \text{ g m}^{-2}$ (or $16.24 \text{ t ha}^{-1} \text{ year}^{-1}$) in the

first year and $3212 \pm 17 \text{ g m}^{-2}$ (or $32.12 \text{ t ha}^{-1} \text{ year}^{-1}$) in the second year. Both values are higher than those reported in the Atlantic Forest ($6.3 \text{ t ha}^{-1} \text{ year}^{-1}$) and in Restinga forest ($3.9 \text{ t ha}^{-1} \text{ year}^{-1}$; Moraes and others 1999) and the $804 \text{ g m}^{-2} \text{ year}^{-1}$ also reported in the Atlantic Forest (Gonçalves and others 2014). The values reported for the total litterfall in non-flooded deciduous and semi-deciduous forests ($7.71 \text{ t ha}^{-1} \text{ year}^{-1}$), and in seasonally flooded evergreen forest ($10.27 \text{ t ha}^{-1} \text{ year}^{-1}$) in the northern Pantanal of Mato Grosso were also smaller than our results (Haase 1999).

Smaller values were also found in studies conducted in the rainforests of central Panama ($1420 \text{ g m}^{-2} \text{ year}^{-1}$; Wieder and Wright 2001) and central Colombia ($703 \text{ g m}^{-2} \text{ year}^{-1}$; Veneklaas 1991), mangrove forest of southern Ecuador ($1055 \text{ g m}^{-2} \text{ year}^{-1}$; Twilley and others 1997), cloud forest of north Venezuela ($532 \text{ g m}^{-2} \text{ year}^{-1}$; Cressa and Weibezahn 1976), and tropical rainforest of Queensland, Australia ($502 \text{ g m}^{-2} \text{ year}^{-1}$). In this study, we observed that the greatest differences in CPOM inputs were found among the months of the year rather than among seasons or years. Some studies have shown that phenological patterns in leaf fall in riparian species are a response to seasonal precipitation (Descheemaeker and others 2006). However, the greatest differences throughout the year are related to seasonal patterns but are not syn-

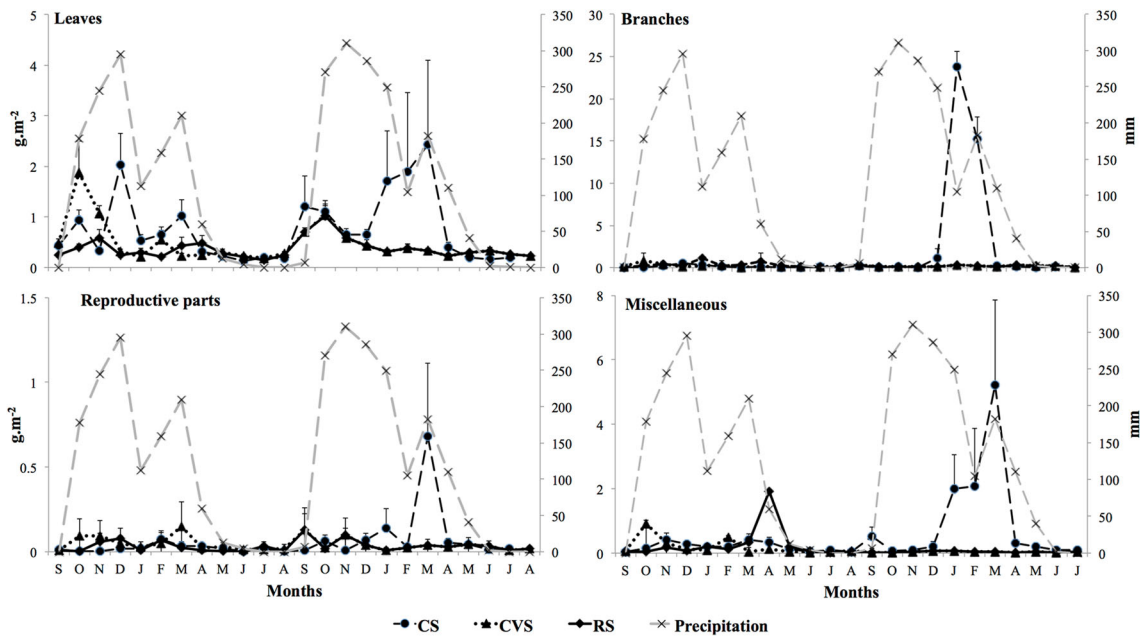


Figure 5. Mean and standard error of CPOM (g m^{-2}) fractions and monthly total precipitation (mm) among September 2010 and August 2012 into the lateral input at pristine streams in Cerrado of Central Brazil.

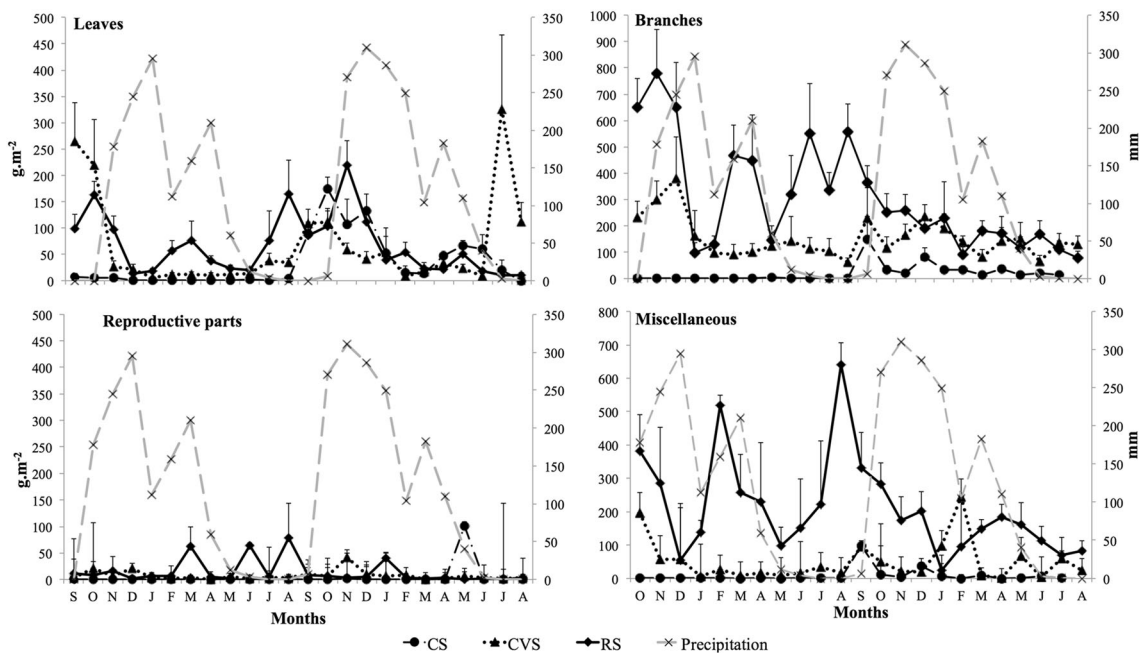


Figure 6. Mean and standard error of CPOM (g m^{-2}) fractions and monthly total precipitation (mm) among September 2010 and August 2012 into the benthic stock at pristine streams in Cerrado of central Brazil.

chronized with climate. Therefore, the CPOM inputs and benthic stock did not change during the dry season but instead increased by the end of the dry season and the beginning of the rainy season during the two years of the study.

This pattern in CPOM inputs is confirmed by most studies conducted in the tropical region regardless of whether they were conducted in upland forests (Wieder and Wright 2001; Sanches and others 2008), dry forests, or in the Amazonian rainforest (Sanches and others 2008; Celentano and others 2011) where water stress is not relevant (Cressa and Weibezahn 1976; Gonçalves and Calisto 2013; Lisboa and others 2015; Rezende and others 2016). As a result, the abscission of leaves may not be determined by differences in precipitation (Poathsin and others 2016). We believe that the factor determining abscission could be the photoperiod, which was shown to influence phenology and phenological responses of plants to seasonal variation in upland forests (Marques and Oliveira 2004; Varejão-Silva 2006). In fact, the photoperiod varies over the course of a year in a more constant way than precipitation throughout the tropical region (Wright and Cornejo 1990): the days become longer in December and shorter in June (Varejão-Silva 2006). In tropical regions, phenological patterns change at the equinox, often with less than a 30-min change in day length (Rivera and Borchert 2001). Because this is the stimulus, this triggering effect is synchronized with day length in the months before the leaves fall (Marques and others 2004), and leaf fall has a close association with the transition to increasing day length with the southern vernal equinox (Marques and others 2004). Unlike the variation in CPOM among months, which is well-discussed in the literature for temperate and tropical regions (Hagen and others 2010), this is the first study performed in the Brazilian savannah addressing inter-annual patterns. Our results indicate that CPOM inputs also vary between years (second year > first), confirming our second hypothesis. However, these differences were not as marked as monthly differences, which are most likely related to the moderate inter-annual differences in precipitation. This annual variation indicates heterogeneity in resource availability in the system, which may also be linked to increases or decreases in the primary productivity of riparian zones (Flombaum and Sala 2008). As a result, the secondary productivity directly linked to plant resource availability in the system may also vary (Odum and Barrett 2005). However, the difference in the amount of CPOM that arrived in the stream through the vertical

(98%) and lateral inputs (2%) between years (second > first year) was not reflected in the variation of CPOM that accumulated in the channel bed. The low rainfall in the first year could have resulted in low water runoff (Jones 1997; Sabater and others 2008) and an increased residence time of the CPOM in the streams, but this did not occur. The benthic stock was similar in both years, which should reflect ecosystem functioning, with a great balance between retention versus transport and respiration (Tank and others 2010), and consequent stability in the ecosystem energy balance.

In this study, the litterfall was mainly composed of leaves, corroborating that they are the major source of energy and nutrient replacement in stream ecosystems (Wantzen and others 2008; Burrows and others 2014; Gonçalves and others 2014). Most studies conducted in headwater streams have made this assumption (leaves are the greatest source of energy) because of canopy overlap, which limits the input of light and, consequently, photosynthesis in the streams (for example, Afonso and Andre 2000; França and others 2009; Carvalho and Uieda 2010; Lisboa and others 2015; Rezende and others 2016). This low in-stream primary productivity induces consumers to use available resources (Brito and others 2006). However, this hypothesis is not well-tested in tropical regions (Bunn and others 1999), and some studies show that even in streams with well-developed riparian vegetation, there might be sufficient penetration of light (Brito and others 2006) to support primary productivity (Bunn and others 1999). In agreement, some recent stable isotopic studies indicate that detritivores assimilate most of their carbon from algae and not from leaf litter (Brito and others 2006). There is an obvious knowledge gap identified in tropical regions that requires further study (Boyero and others 2009).

Branches are the second most abundant fraction of the CPOM inputs and the first of the benthic stock in this study. This result, which was also noted by Brito and others (2006), is contrary to what is commonly described in the literature, which indicates that branches are also the second fraction in the benthic stock (for example, Afonso and Andre 2000; França and others 2009; Carvalho and Uieda 2010; Lisboa and others 2015; Rezende and others 2016). A higher contribution of branches can limit the availability of energy for aquatic biota due to their low nutritional quality (Elosegi and others 2007). However, branches have an important role in the stability of stream channels and habitat formation (by retaining leaves), supporting a wide variety of organisms at different stages of their life cycles

(Steiger and Gurnell 2002). The reproductive parts of plants have low biomass, but this fraction is quite important because of its high nutrient concentration compared to that of leaves and branches (Elosegi and Pozo 2005).

We found also spatial differences in CPOM patterns at a small linear distance (maximum 7.5 km). Although the RS (in the middle section of the drainage basin) and the CVS (downstream in the drainage basin) were similar in terms of their leaf fractions and benthic stocks, the CS (upstream in the drainage basin) vertical and terrestrial components had lower masses. This could be due to the different topography of this stream (irregular topography and deep valley compared to flat valleys), which results in a drier riparian soil and a low plant density. The steep banks could also have led to the higher lateral input due to greater runoff (Kochi and others 2010). On the other hand, it was at the CS that some samples were washed away by torrential rains.

CONCLUSIONS

In conclusion, monthly CPOM inputs in the streams are continuous in small amounts with peaks occurring in the transition period between seasons. There are some peaks during the rainy season associated with spatial variation in inputs of CPOM, although the sites are in the same watershed. The spatial variation in CPOM inputs from riparian areas in the same watershed is determined by topographic and hydrological characteristics of the streams. In riparian vegetation and forests where water stress has low importance (as a result of higher variation over the longer term), the photoperiod may be the most important evolutionary factor determining monthly patterns in CPOM, as precipitation only partially explains its variation. The variation in benthic stock between years suggests the stability of retention versus transport and respiration, ensuring a balance in energy and stream functioning regardless of the heterogeneity of allochthonous productivity. The difference in CPOM between years revealed heterogeneity in resource availability that could lead to fluctuations in secondary productivity. Thus, CPOM models from one year cannot be linearly transposed to another year. Longer-term studies are needed to clarify this temporal pattern. This study represents an advancement in the understanding of CPOM input patterns into streams in tropical regions, especially in the Brazilian savannah (Cerrado) biome.

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