



Post-fire consequences for leaf breakdown in a tropical stream

Consequências do pós-fogo para a decomposição foliar em riachos tropicais

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Abstract: Aim: Wildfire is a natural pulsed disturbance in landscapes of the Savannah Biome. This study evaluates short-term post-fire effects on leaf litter breakdown, the invertebrate community and fungal biomass of litter from three different vegetal species in a tropical stream. **Methods:** Senescent leaves of *Inga laurina*, *Protium spruceanum* and *Rircheria grandis* (2 ± 0.1 g dry mass) were individually placed in litter bags (30×30 cm: 10 mm coarse mesh and 0.5 mm fine mesh) and submerged in the study stream before and after fire. Replicate bags ($n = 4$; individually for each species, sampling time, fire event and mesh size) were then retrieved after 20 and 40 days and washed to separate the invertebrates before fire event and again immediately after fire. Disks were cut from leaves to determine ash-free dry mass, while the remaining material was oven-dried to determine dry mass. **Results:** The pre-fire mean decomposition coefficient ($k = -0.012 \text{ day}^{-1}$) was intermediate compared to that reported for other savannah streams, but post-fire it was lower ($k = -0.007 \text{ day}^{-1}$), due to decreased allochthonous litter input and increased autochthonous production. Intermediate k values for all qualities of litter post-fire may indicate that fire is equalizing litter quality in the stream ecosystem. The abundance of scrapers was found to be more important than fungal biomass or shredder abundance, probably due to their functioning in leaf fragmentation while consuming periphyton growing on leaf litter. **Conclusions:** These results indicate that fire can modify the relationships within decomposer communities in tropical stream ecosystems.

Keywords: litter decomposition; indirect fire effects; allochthonous litter; short-time scale.



Resumo: Objetivo: Queimadas é um distúrbio natural nas paisagens do Bioma Savana. Este estudo avalia os efeitos do pós-fogo (antes e depois) na decomposição de serapilheira na comunidade de invertebrados e biomassa de fungos em diferentes detritos e malhas (fina e grossa) em riacho em curto prazo temporal. **Métodos:** Folhas senescentes ($2 \pm 0,1$ g de peso seco) foram colocadas em sacos (30×30 cm, 10 mm – de malha grossa e 0,5 mm - de malha fina) e submersas no fluxo antes e depois do fogo. Sacos replicados ($n = 4$) foram recuperados após 20 e 40 dias e lavados em uma peneira para separar os invertebrados (densidade, riqueza e grupo trófico funcional) para ambos os tratamentos (antes e após o fogo). Uma série de discos das folhas foi cortada para determinar a massa seca isenta de cinzas e o material restante foi seco em estufa para determinar o peso seco. **Resultados:** O coeficiente médio de decomposição ($k = -0,012 \text{ dia}^{-1}$ antes do fogo) corresponde ao intervalo intermediário observado em outros riachos de Savana, com valores menores no pós-fogo ($k = -0,007 \text{ dia}^{-1}$). Isso pode ser explicado pelo fogo diminuir a importância da serapilheira alóctone para metabolismo de fluxo devido a aumentar a produção de autóctones (maior abertura do dossel pela queima do mesmo). O coeficiente de decomposição intermediário de todas as diferentes espécies de folhas pós-incêndio pode indicar que o fogo pode equalizar a qualidade da serapilheira em ecossistemas de lóticos. Por outro lado, raspadores (e não fungos ou fragmentadores) pela função de fragmentação foliar (por consumo de perifíton) diminuíram sua abundância (30-50%) no pós-fogo como a perda de massa foliar. **Conclusões:** Isso pode indicar que o pós-fogo modifica as relações de importância dentro das comunidades decompositoras em riachos tropicais.

Palavras-chave: decomposição foliar; efeitos indiretos do fogo; serapilheira alóctone; escala de tempo curto.

1. Introduction

Wildfire is a natural pulsed disturbance in landscapes of the Cerrado (Neotropical savannah) biome in Brazil (Ribeiro, 2008); however, a warming climate can increase the frequency and intensity of wildfire disturbance (Rodríguez-lozano et al., 2015; Silverio et al., 2013). Some of the effects that fire has on freshwater ecosystems (e.g. increased rate of nutrient cycling and changes to the trophic chain and physical and chemical properties of the water) may be similar to those from anthropic land use, such as agricultural and silviculture (for more see Bixby et al., 2015). The frequency of fire disturbance in riparian vegetation of Cerrado *stricto sensu* (Silverio et al., 2013), is low or absent due to its higher humidity (Bixby et al., 2015). The direct impact most commonly caused by fire is to the physical structure of the marginal aquatic ecosystem, which suppresses riparian vegetation (Pettit & Naiman, 2007; Verkaik et al., 2013). Consequently, burned vegetation processes lower riparian canopy cover than non-burned vegetation, which increases water temperature due to higher luminosity (Rodríguez-Lozano et al., 2015). Wildfire changes water quality with consequences for aquatic communities and ecosystem processes (Pettit & Naiman, 2007; White-Monsant et al., 2017). For example, the effects of fire can change the dynamics of organic matter (OM), and consequently nutrient cycling in streams by damaging or killing upland vegetation (Earl & Blinn, 2003). The effects of fire may also be driven

by resilient successional trajectories for watershed recovery (Bixby et al., 2015; White-Monsant et al., 2017), with changes to OM dynamics (e.g. leaf litter breakdown) in riparian zones during this process (Rodríguez-Lozano et al., 2015).

Allochthonous leaf litter breakdown is important for the maintenance of the metabolism of small-order streams (Tank et al., 2010). However, fire can favor runoff and erosion, which increases changes to leaf breakdown rates (Earl & Blinn, 2003; Watts & Kobziar, 2015). The duration of the effects of fire depends on vegetation recovery, since it causes an increase in light and temperature (Bixby et al., 2015). Vegetation suppression may also increase autochthonous input, and thus change functioning of the stream ecosystem (Cooper et al., 2015). Therefore, increased light levels (i.e., autochthonous production) associated with increased inorganic nutrients (from fire mineralization) may affect leaf breakdown rates and the density of associated communities in stream ecosystems (Verkaik et al., 2015; Whitney et al., 2015). Nonetheless, there have been few studies on the effects fire has on stream ecosystem processes due to the low number of fire events in riparian vegetation, with tropical systems being particularly poorly understood (Rodríguez-Lozano et al., 2015).

Studies of the effects of fire on freshwater ecosystems have considered a wide variety of organisms (e.g., fish, invertebrates and vegetation) in many areas and biomes (Bixby et al., 2015), but rarely, South America streams (Bixby et al., 2015;

Dwire & Kauffman, 2003; Pettit & Naiman, 2007; Reale et al., 2015). This is surprising given the recent increase in wildfire events (in frequency and intensity) due to climate change (Rodríguez-Lozano et al., 2015). Studies of the effects of fire mainly address physical-chemical processes (e.g. hydrology, and biogeochemistry; Brown et al., 2015; Watts & Kobziar, 2015) or other terrestrial-aquatic interactions (Douglas et al., 2015; Reale et al., 2015), but ecological processes (e.g. leaf breakdown rates) are often overlooked (Rodríguez-Lozano et al., 2015).

Leaf litter breakdown is typically driven by the microbial community (mainly fungi and bacteria) along with invertebrate shredders (Gonçalves-Júnior et al., 2014; Graça et al., 2015); however, shredders are scarce in tropical streams, and the microbial community becomes the dominant decomposer of litter (Rezende et al., 2018a, 2015; Rezende et al., 2014). The bacteria community makes a greater contribution to decomposition in the initial stages due their high capacity to degrade soluble compounds of leaves, including carbohydrates, phenols and tannins (Alvim et al., 2015; Gonçalves-Júnior et al., 2006). On the other hand, aquatic hyphomycetes make a greater contribution to the final of decomposition due to their high capacity for degrading structural compounds such as lignin and cellulose (Graça et al., 2016, 2015). Leaf quality is another important factor that influences decomposer activity (Tank et al., 2010). In tropical streams, leaf litter with higher concentrations of nutrients (e.g. nitrogen and phosphorus) and labile compounds is likely to be broken down more rapidly compared to litter with high leaf hardness and more structural compounds (Gonçalves-Júnior et al., 2016; Rezende et al., 2014).

Based on the premise that: i) allochthonous inputs increase from damaged vegetation after riparian fires, and subsequently decrease due to riparian vegetation loss (Britton, 1990; Cooper et al., 2015); ii) this initial input of leaf organic matter may eventually rebound as riparian vegetation recovers (Britton, 1990; Cooper et al., 2015; Rodríguez-Lozano et al., 2015), increasing the autochthonous production by inputs of inorganic nutrients (Cooper et al., 2015); iii) increased of light levels (and thus autochthonous production), associated with nutrient contributions (by fire mineralization), may decrease the importance of leaf breakdown for stream metabolism and slow the rate of decomposition; and iv) leaf quality is

an important factor for control of decomposer activity and for providing variation in leaf chemical characteristics (soluble and structural compounds in litter), which drive the use by the decomposer community. Our first hypothesis is that fire slow down the rate of leaf breakdown in stream because it increases autochthonous production therein. The second hypothesis is that low quality leaf litter (more structural, and fewer secondary, compounds) will be broken down more slowly than higher quality litter. Our third hypothesis is that the litter quality is of more importance to fungal and invertebrate communities than the effects of fire. Thus, our aim was to measure the effects of fire on leaf litter breakdown, the invertebrate community and fungal biomass in leaf litter three different plant species (*Inga laurina*, *Protium spruceanum* and *Rircheria grandis*) in a tropical stream.

2. Materials and Methods

2.1. Study area

The study was carried out in Bacaba stream (14°43'12.95"S, 52°21'34.62"W; Bacaba stream; Figure 1) located in an area of transition between Savannah (Cerrado) and Amazon Rainforest. According to Köppen, the regional climate is Tropical Savannah (Aw), with Monsoon (Am) and Tropical Rainy (A) subtypes regions. The dry season is from May to October, while the rainy season is from November to April. Annual rainfall ranges from 1500 to 1800 mm with a mean of 1400 mm (greater than typical Brazilian Savannah), while the temperature ranges from 17 to 34 °C.

2.2. Procedures

Initial (before incubation) leaves of *Protium spruceanum*, *Rircheria grandis* and *Inga laurina* were dried at 60 °C for 48h (to constant weight), weighed in a precision balance and pulverized in a mill for analysis of secondary compounds (total polyphenol and tannic acid concentration; Bärlocher & Graça 2005). Structural compounds (lignin and cellulose) were determined gravimetrically following the procedure of Gessner (2005a). Values for total nitrogen were obtained using a CHN basic analyzer (Carlo Erba 1500 for WI; Thermo Electron Corp. Milan, Italy; Allen et al., 1974) while those for total phosphorus were acquired by the ascorbic acid method after acid digestion (Fassbender, 1973).

Leaves of *I. laurina* had higher values for recalcitrant compounds, such as lignin (45.94 ± 0.5%) and cellulose (37.39 ± 1.2%), compared to *R. grandis* (30.4 ± 0.9 and 28.9 ± 1.9%) and *P. spruceanum*



Figure 1. Post-fire condition of vegetation in an adjacent area (A) and into the riparian zone (B and C) of a stream in an ecotone between Cerrado and Tropical Rain Forest.

(39.1 ± 0.9 and $33.2 \pm 0.7\%$; respectively). Leaves of *I. laurina* also had higher values for nutrients, such as nitrogen ($16.41 \pm 1.0 \text{ g.g}^{-1}$) and phosphorus ($0.53 \pm 0.07 \text{ g.g}^{-1}$), than *R. grandis* (8.4 ± 0.9 and $0.29 \pm 0.04 \text{ g.g}^{-1}$) and *P. spruceanum* (8.2 ± 1.1 and $0.34 \pm 0.09 \text{ g.g}^{-1}$, respectively). Leaves of *P. spruceanum* on the other hand, had higher values for secondary compounds (water soluble), such as total polyphenols ($54.5 \pm 3.2 \text{ mg.g}^{-1}$) and total tannic acids ($0.006 \pm 0.0012 \text{ mg.g}^{-1}$), compared to *R. grandis* (21.8 ± 2.3 and $0.003 \pm 0.0007 \text{ g.g}^{-1}$) and *I. laurina* (18.29 ± 1.8 and $0.002 \pm 0.0004 \text{ g.g}^{-1}$, respectively). Thus, the leaf litter from the leaves of the three species can be categorized (only for the studied system) as of higher quality for *R. grandis*, intermediate quality for *P. spruceanum* and low quality for *I. laurina*.

Leaves used for the experiment were dried at room temperature until a constant mass was achieved. Litter bags ($10 \times 20 \text{ cm}$) of two mesh sizes (10 mm for coarse and 0.5 mm for fine) were prepared with 2 g (± 0.1) of dry leaves of one of the species each. Four litter bags (sub-samples) for each species (individually) were incubated during August to September 2016 (before fire) and November to December 2016 (after fire) for 20 and 40 days for two sampling times. The samples were then removed and placed individually into insulated plastic bags and transported in thermal containers to the laboratory where they were transferred to a refrigerator ($4 \text{ }^\circ\text{C}$) until processing. Temperature, electrical conductivity, pH, dissolved oxygen, total dissolved solids, water turbidity and oxidation/reduction potential of the water was

measured *in situ* with a multi-analyzer at the time each litter bag was recovered from the stream. Nitrate, nitrite, ammonium and phosphorous were obtained in laboratory by spectrophotometric analysis according to APHA (2015).

In the laboratory, leaves of *P. spruceanum*, *R. grandis* and *I. laurina* from the litter bags were washed with water in a 120 mm mesh sieve: invertebrates retained on the sieve were preserved in 70% alcohol for later identification (Cummins et al., 2005; Cummins, 1996; Hamada et al., 2014). The number of *taxa* (richness) and individuals (density) of invertebrate were calculated for the aquatic invertebrate community. The invertebrate were then classified into five feeding categories: gathering-collectors, filtering-collectors, shredders, scrapers, and predators (Cummins et al., 2005; Cummins, 1996; Hamada et al., 2014; Hamada & Ferreira-Keppler, 2012; Martínez et al., 2013; Pérez, 1988). Of these categories, only the occurrence and frequencies of shredders and scrapers were used to determine the direct effects on leaf litter.

Leaves from each litter bag were randomly collected, and two disks (1.2 cm in diameter; resulting in two five-disk sets) was extracted from a randomly selected leaf from each litter bag for determining remaining ash-free dry mass (AFDM; calculated after incineration in a muffle furnace at 550 °C for 4 h) and biomass of aquatic hyphomycetes (by quantifying ergosterol that are a lipid exclusive to fungal membranes, according to Gessner, (2005b)). The remaining material was oven-dried at 60 °C for 72 h to determine its dry mass (Graça et al., 2005).

2.3. Statistical analysis

Normality of the data was analyzed with the Shapiro-Wilk normality test, and the Kolmogorov-Smirnov test, while homogeneity of variances was assessed with Levene's test. Data were Ln (+1) transformed or with the root sine arc of the ratio to obtain the best fit for percentage data if needed. Leaf litter breakdown rates (k) were calculated using a negative exponential model of the percent of mass lost over time ($W_t = W_0 e^{-kT}$; W_t = remaining weight; W_0 = initial weight; $-k$ = decay rate; t = time).

We tested the remaining mass, density and richness of invertebrates, abundance of shredders and ergosterol concentration (dependent variables) between treatments (before and after fire) and among leaf litter species (*P. spruceanum*, *R. grandis* and *I. laurina*) and the interaction between these two

factors (response variables) by a factorial two-way repeated measures ANOVA (RM-ANOVA). The RM-ANOVA was conducted using time in days (20 and 40 days) as repeated measurements (Crawley, 2007), building one statistical model for mesh sizes (coarse and fine) separately from each dependent variable. RM-ANOVA is usual in experiments with different error variances and correction for pseudoreplication (see chapter 11 of Crawley (2007)). The abiotic variables were tested between treatments (before and after fire) using a one-way ANOVA.

Differences among the categorical variables were assessed through a contrast analysis (Crawley, 2007). In this contrast analysis (orthogonal), the dependent variables of different sampling times and leaf litter quality were ordered (increasingly) and tested pairwise (with the closest values). Sequentially this dates are adding to the model values with no differences and testing with the next in a steps model simplification (for more see also chapter 9 of Crawley (2007)).

The specific contribution of invertebrates to leaf litter breakdown was estimated by the difference between the AFDM remaining in total (coarse-mesh) and microbial (fine-mesh) leaf breakdown bags at each sampling time; a new k value was then calculated. However, according to Tonin et al. (2017) total leaf breakdown (coarse-mesh) cannot be estimated by summing microbial (fine-mesh) and invertebrate leaf breakdown rates because they do not account for interactions between decomposers and invertebrates.

3. Results

3.1. Leaf litter breakdown rates and water physico-chemical characteristics of the water

Stream water was acid (pH before 4.5 ± 0.03 and after 4.7 ± 0.21 fire; mean \pm standard error), with low levels of oxygen (6.1 ± 0.31 and 4.6 ± 0.87 mg.l⁻¹), electrical conductivity (0.04 ± 0.001 and 0.02 ± 0.004 mS.cm⁻¹), turbidity (2.9 ± 0.32 and 8.4 ± 2.41 NTU), and total dissolved solids (0.03 ± 0.003 and 0.01 ± 0.002 g.l⁻¹). Nitrite values (before: 0.11 ± 0.02 and after: 0.04 ± 0.004 mg.l⁻¹) decreased after fire while water discharge (0.05 ± 0.01 and 0.18 ± 0.02 m.s³), water temperature (23.5 ± 0.38 and 26.5 ± 0.22 °C), nitrate (1.8 ± 0.14 and 2.3 ± 0.24 mg.l⁻¹), ammonium (0.16 ± 0.03 and 0.17 ± 0.03 mg.l⁻¹), and phosphorus (0.11 ± 0.01 and 0.16 ± 0.06 mg.l⁻¹) all increased after fire. However, only total dissolved solids (ANOVA; $F_{(1,16)} = 6.75$; $p = 0.047$), water temperature

(ANOVA; $F_{(1,16)} = 24.41$; $p = 0.001$) and nitrite (ANOVA; $F_{(1,16)} = 6.19$; $p = 0.049$) differed significantly between treatments.

The total mean of decomposition coefficient (k , Figure 2) was higher before fire (-0.012 d^{-1}) that after (-0.007 d^{-1}), ranging from -0.005 (*I. laurina* in fine mesh after fire) to -0.015 (*P. spruceanum* in coarse mesh before fire). The remaining mass in fine mesh was mostly *I. laurina* (71.5 and 84.5%), followed by *P. spruceanum* (70.1 and 78.1%) and *R. grandis* (64.9 and 69.7%), before and after fire,

respectively. The remaining mass in coarse mesh was mostly *R. grandis* (70.3%) followed by *I. laurina* (66.3%) and *P. spruceanum* (56.7%) before fire. Finally, the remaining mass after fire in coarse mesh is higher in *I. laurina* (83.9%), followed to *P. spruceanum* (77.6%) and *R. grandis* (71.2%). Differences in remaining mass among leaf species were observed in both meshes, with higher values in *I. laurina* compared to *R. grandis* and *P. spruceanum* (Figure 2; Table 1; contrast analysis > 0.05). The interaction between treatment and leaf litter

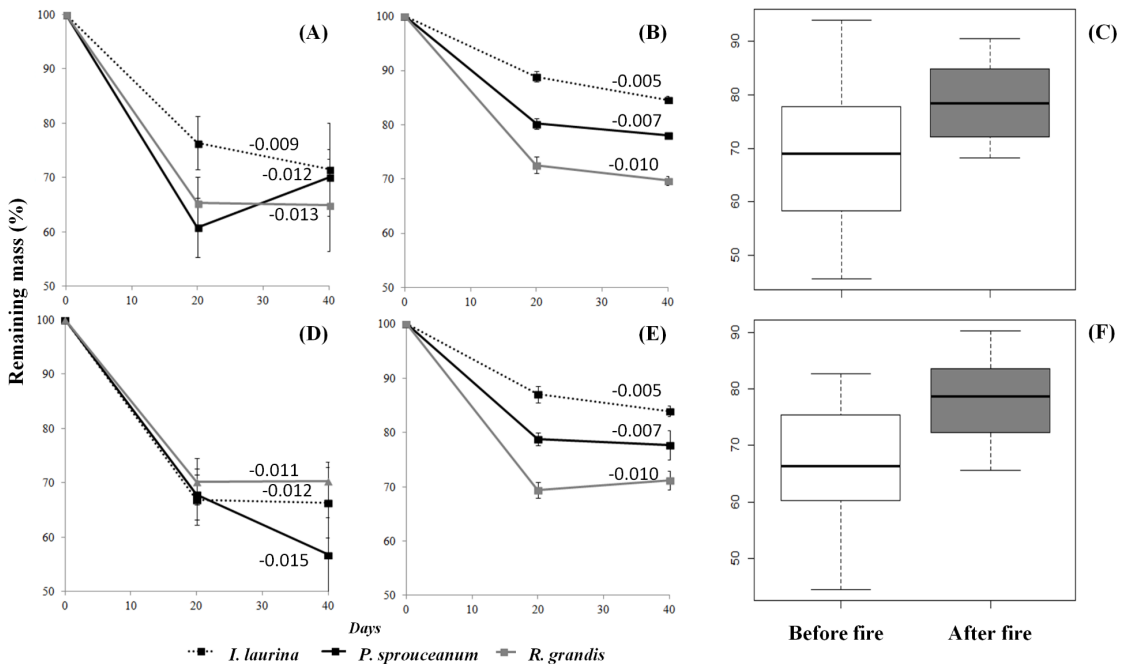


Figure 2. Remaining mass (%) in fine (A, B and C) and coarse (D, E and F) mesh litter bag before (A, D and white in C and F) and after (B, E and gray in C and F) fire for leaf litter of *I. laurina*, *P. spruceanum* and *R. grandis* in a stream in a ecotone between Savannah and Tropical Rain Forrest stream. The negative numbers are k values.

Table 1. Results from RM-ANOVA and contrast analysis ($P < 0.05$) of remaining mass in fine (A) and coarse (B) mesh litter bags, shredder abundance (C), scrapers abundance (D), total invertebrate richness (E), total invertebrate density (F), Ergosterol in in fine (G) and coarse (H) mesh litter bags between two treatments (before and after fire), for leaf litter from three species (*R. grandis*, *P. spruceanum* and *I. laurina*), and the interaction between factors.

RM-ANOVA	Df	Sum Sq %	F	Pr(>F)	Contrast analysis
A. Remaining mass (%) in FM					
Residuals Error: Days	1	0.15			
Treatment	1	23.05	17.39	< 0.001	Before < After
Leaf Litter	2	20.16	7.61	0.002	<i>R. grandis</i> = <i>P. spruceanum</i> < <i>I. laurina</i>
Treatment: Leaf Litter	2	2.29	0.86	0.429	
Residuals	41	54.35			

FM = fine mesh; CM = coarse mesh; Df = degree of freedom; Sum Sq % = sums of squares percentage; F = F test; Pr(>F) = significance by F test.

Table 1. Continued...

RM-ANOVA	Df	Sum Sq %	F	Pr(>F)	Contrast analysis
B. Remaining mass (%) in CM					
Residuals Error: Days	1	1.24			
Treatment	1	30.81	27.76	< 0.001	Before < After
Leaf Litter	2	6.81	3.07	0.049	<i>R. grandis</i> = <i>P. spruceanum</i> < <i>I. laurina</i>
Treatment: Leaf Litter	2	15.63	7.04	0.002	
Residuals	41	45.50			
C. Shredder (%)					
Residuals Error: Days	1	3.34			
Treatment	1	8.78	4.68	0.036	Before < After
Leaf Litter	2	3.86	1.03	0.367	
Treatment: Leaf Litter	2	7.02	1.87	0.167	
Residuals	41	77.00			
D. Scrapers (%)					
Residuals Error: Days	1	0.00			
Treatment	1	0.12	0.05	0.810	
Leaf Litter	2	3.43	0.85	0.433	
Treatment: Leaf Litter	2	14.13	3.51	0.038	
Residuals	41	82.33			
E. Richness of invertebrates					
Residuals Error: Days	1	0.66			
Treatment	1	11.21	6.09	0.017	Before < After
Leaf Litter	2	0.07	0.02	0.982	
Treatment: Leaf Litter	2	12.64	3.44	0.042	
Residuals	41	75.42			
F. Density of invertebrates					
Residuals Error: Days	1	1.35			
Treatment	1	8.50	4.44	0.041	Before < After
Leaf Litter	2	10.89	2.84	0.070	
Treatment: Leaf Litter	2	0.70	0.18	0.833	
Residuals	41	78.55			
G. Ergosterol in FM					
Residuals Error: Days	1	11.83			
Treatment	1	35.36	12.40	0.009	Before < After
Leaf Litter	2	1.03	0.36	0.566	
Treatment: Leaf Litter	2	31.79	11.14	0.012	
Residuals	41	19.96			
H. Ergosterol in CM					
Residuals Error: Days	1	15.21			
Treatment	1	21.05	3.26	0.114	
Leaf Litter	2	8.38	1.31	0.291	
Treatment: Leaf Litter	2	10.26	1.59	0.247	
Residuals	41	45.08			

FM = fine mesh; CM = coarse mesh; Df = degree of freedom; Sum Sq % = sums of squares percentage; F = F test; Pr(>F) = significance by F test.

was significant only for coarse-mesh. Finally, most of the variance in fine-mesh was explained (sum of squares) by treatments, followed by leaf litter species while in coarse-mesh it was explained by the interaction factor (Table 1; Figure 2).

3.2. Decomposer community

Invertebrate density ranged from 2.2 ind.g⁻¹ for *I. laurina* before fire to 3.9 ind.g⁻¹ for *P. spruceanum* after fire (Table 2). The most abundant *taxon* was the family Chironomidae and the class Oligochaeta

(Table 2). Mean species richness (number of *taxa*) was six *taxon*, ranging from eight for *I. laurina* after fire to four for *I. laurina* before fire. The invertebrate communities had greater density and species richness after fire (Table 1; Figure 3). The density of shredders was also present higher after fire than before (Table 1; Figure 3 and 4). On the other hand, the density of scrapers did not differ among treatments, but differed significantly for the interaction between treatment and litter quality,

Table 2. Mean (ind.g⁻¹) and standard error (±) for invertebrates in litter of *I. laurina*, *P. spruceanum* and *R. grandis* before and after fire in a tropical stream system.

	Before fire			After fire		
	<i>I. laurina</i>	<i>P. spruceanum</i>	<i>R. grandis</i>	<i>I. laurina</i>	<i>P. spruceanum</i>	<i>R. grandis</i>
Platyhelminthes	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.34 ± 0.67	5.17 ± 1.75	1.41 ± 0.56
Annelida						
Hyrundinae	0.00 ± 0.00	1.74 ± 0.32	0.00 ± 0.00	0.08 ± 0.06	0.18 ± 0.08	0.00 ± 0.00
Oligochaeta	13.96 ± 4.19	33.33 ± 7.18	22.68 ± 5.28	17.46 ± 4.45	21.60 ± 5.45	10.01 ± 2.16
Mollusca						
Gastropoda						
Ancyliidae	19.54 ± 4.41	15.69 ± 2.18	15.10 ± 2.86	14.79 ± 2.25	32.08 ± 4.82	18.25 ± 5.25
Arthropoda						
Chelicerata						
Arachnida						
Hydracarina	0.13 ± 0.09	0.10 ± 0.07	0.00 ± 0.00	0.24 ± 0.09	0.26 ± 0.14	0.78 ± 0.29
Crustacea						
Ostracoda	1.09 ± 0.53	2.85 ± 0.69	0.89 ± 0.29	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Hexapoda						
Insecta						
Ephemeroptera						
Caenidae	0.59 ± 0.34	1.15 ± 0.42	0.00 ± 0.00	1.11 ± 0.35	0.26 ± 0.09	0.97 ± 0.32
Baetidae	0.00 ± 0.00	0.00 ± 0.00	0.35 ± 0.17	0.24 ± 0.12	0.53 ± 0.38	2.42 ± 0.85
Odonata						
Coenagrionidae	0.13 ± 0.09	0.28 ± 0.21	0.85 ± 0.27	2.45 ± 1.07	0.34 ± 0.14	2.12 ± 0.59
Libellulidae	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.55 ± 0.28	0.09 ± 0.06	0.39 ± 0.15
Calopterygidae	0.00 ± 0.00	0.00 ± 0.00	0.27 ± 0.20	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Aeshnidae	0.11 ± 0.08	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Trichoptera						
Hydroptilidae	0.00 ± 0.00	0.10 ± 0.07	0.19 ± 0.09	0.08 ± 0.06	0.09 ± 0.06	0.10 ± 0.08
Coleoptera						
Dytiscidae	0.47 ± 0.23	1.20 ± 0.47	0.37 ± 0.15	1.75 ± 0.71	1.92 ± 0.90	2.02 ± 0.58
Elmidae	0.11 ± 0.08	0.00 ± 0.00	0.09 ± 0.07	0.07 ± 0.05	0.09 ± 0.06	0.00 ± 0.00
Diptera						
Chironomidae	5.57 ± 1.32	12.29 ± 3.20	7.65 ± 1.49	28.78 ± 5.55	35.22 ± 5.14	24.12 ± 4.85
Ceratopogonidae	0.16 ± 0.12	0.28 ± 0.21	0.30 ± 0.15	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Total mean	2.46 ± 0.68	4.06 ± 0.88	2.87 ± 0.65	4.05 ± 0.92	5.75 ± 1.12	3.68 ± 0.92

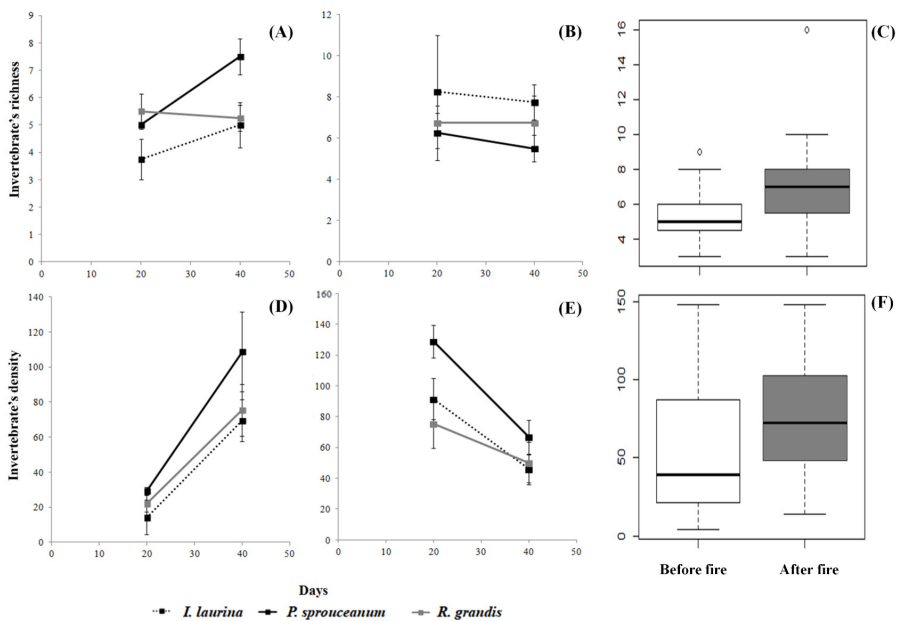


Figure 3. Invertebrate richness (A, B and C) and density (D, E and F) among different leaf litter (A, B, D and E) before (A, C and white in C and F) and after fire (B, D and gray in C and F) in a stream in a ecotone between Savannah and Tropical Rain Forrest.

with higher values for higher quality leaf before fire (Table 1; Figure 3 and 4).

The mean (\pm SE) concentration of ergosterol (fungal biomass) was $83 \pm 11 \mu\text{g}\cdot\text{g}^{-1}$, with a maximum of $130 \mu\text{g}\cdot\text{g}^{-1}$ for *P. spruceanum* in coarse mesh before fire, and a minimum of $43 \mu\text{g}\cdot\text{g}^{-1}$ for *I. laurina* in fine mesh after fire. This difference was significant only for treatments in fine mesh before and after fire with higher values after fire (Table 1; Figure 5; Contrast analysis > 0.05). The sum of squares percentage revealed that most of the variance was explained by treatments followed by

the interaction factor and leaf litter species for both meshes (Table 1).

4. Discussion

4.1. Post-fire effects on leaf litter breakdown process

Decreased canopy cover may have stimulated algae production (Cooper et al., 2015; Rezende et al., 2017), which would explain the significant decrease (by algae biomass incorporation) in total dissolved solids and nitrite post-fire in the studied stream. Therefore, we hypothesize that increased autochthonous production can decrease the importance of allochthonous production (Lau et al., 2008; Rezende et al., 2017). This supposition is corroborated by the low use of litter as food resource by the aquatic community (microbial and shredder invertebrates) observed in the present study. Therefore, the suppression of riparian vegetation by fire decreased the leaf mass loss post-fire for the short-term, despite higher shredder density and microbial biomass.

The slow post-fire leaf litter breakdown observed in the studied stream is in contrast to what has been reported for temperate streams systems (Rodríguez-Lozano et al., 2015; Verkaik et al., 2013). However, these authors investigated the effects on leaf litter breakdown (increased rates) for more than two years post-fire, which may explain the different results of the present study (decreased

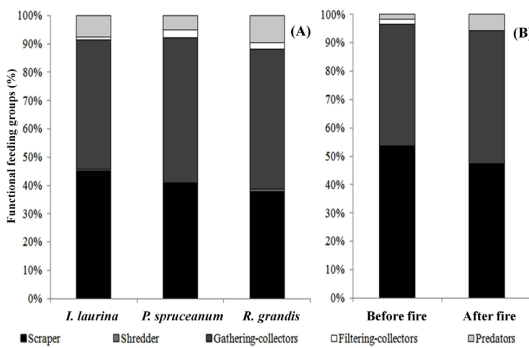


Figure 4. Percentage of functional feeding groups among different leaf litter (A) before and after fire (B) in a stream in an ecotone between Savannah and Tropical Rain Forrest.

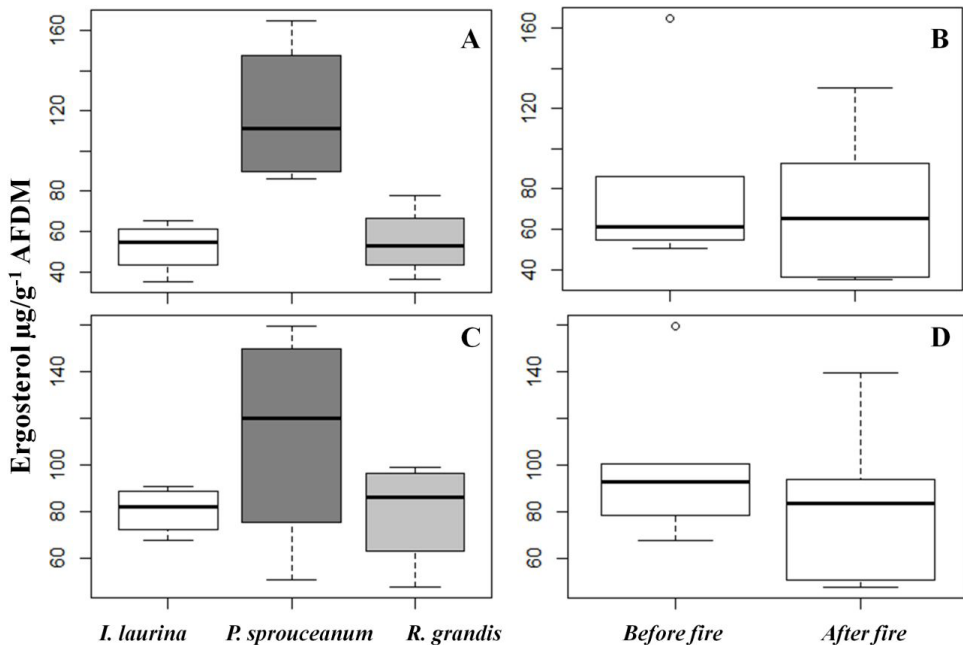


Figure 5. Fungal biomass (Ergosterol $\mu\text{g}\cdot\text{g}^{-1}$) in fine (A and B) and coarse (C and D) mesh litter bags for different leaf litter (A and C) before and after fire (B and C) in a stream in an ecotone between Savannah and Tropical Rain Forrest.

rates), which investigated immediate post-fire effects. This may also explain the importance of variation in autochthonous-allochthonous production to Cerrado stream metabolism (Lau et al., 2008; Rezende et al., 2017; Wagner et al., 2017). On the other hand, the decomposer community recovered quickly after fire (Rodríguez-Lozano et al., 2015), using the leaf litter mainly as a substrate (Rezende et al., 2016; Uieda & Carvalho, 2015). However, since long-term effects, were not investigated, they remain obscure for Cerrado (tropical) stream systems and thus warrant further investigation.

Litter quality was of less significance than fire treatments. Therefore, post-fire drives the general pattern in immediately post-fire events for this ecological process in the study area, as also observed for other systems (Rodríguez-Lozano et al., 2015; Verkaik et al., 2013). The lower importance of litter quality compared to post-fire effects is corroborated by the higher explanation of variance (by sum squares) between treatments for both mesh size. In contrast, lower breakdown rates were found for *I. laurina* than *R. grandis* and *P. spruceanum* for both mesh sizes. The low decomposition of the leaf litter of *I. laurina* was most likely a consequence of its high content of structural compounds (lignin and cellulose) and relative hardness (cuticle thickness), which hinder the release of other chemical compounds (e.g., polyphenols, nitrogen and phosphorus (Gonçalves-Júnior et al., 2016; Rezende et al., 2014, 2017). This may explain the lower mean density of invertebrates (2.2–3.9 ind.g⁻¹ AFDM) than reported for other savannah streams systems (2–780 ind.g⁻¹; Gonçalves-Júnior et al., 2012a; Ligeiro et al., 2010; Moretti et al., 2007; Rezende et al., 2014, 2017, 2016). Therefore, the chemical characteristics of leaf litter may drive the speed of leaf processing, with breakdown rates increasing with increasing litter quality.

Microbially mediated leaf breakdown (fine-mesh) was of lower importance than total (microbial + shredder + scrapers + water discharge) leaf breakdown (coarse-mesh), mainly before fire (corroborated by the specific *k* for invertebrates). The frequency of shredders (mean 0.5%, range 0–2%) was lower, while that of scrapers (mean 41%, range 34–53%) was higher than that observed in other tropical streams (7–30%, excluding chironomids; Gonçalves-Júnior et al., 2012a; Ligeiro et al., 2010; Moretti et al., 2007; Rezende et al., 2014, 2017, 2016). This can be explained by increased aggregation of scrapers

(before fire) in coarse-mesh leaf bags (Rezende et al., 2018b, 2010). The greater importance of scrapers than shredders is a recurrent finding for tropical aquatic systems (Gonçalves-Júnior et al., 2016; Rezende et al., 2018b, 2017, 2010). Scrapers function in leaf fragmentation in stream systems by using a scraping apparatus, such as a radula to consume periphyton prior to fire (Casas & Gessner, 1999; Gonçalves-Júnior et al., 2016; Rezende et al., 2018b, 2017, 2010). The reproduction of many scrapers (semi-aquatic such as gastropods) is dependent on adjacent plant systems (Cummins et al., 2005; Hamada et al., 2014), which explains low scraper density after fire. Therefore, post-fire conditions may modify the relationships of relative importance within decomposer communities over the short-term scale (Cooper et al., 2015; Rodríguez-Lozano et al., 2015), particularly in tropical stream systems.

Finally, the recorded decomposition coefficients (*k*) ranged from -0.005 to -0.015 day⁻¹, which can be considered intermediate (-0.004 > *k* < -0.017 day⁻¹), according to the model proposed by (Gonçalves-Júnior et al., 2014) for tropical streams. The mean *k* before (-0.012 day⁻¹) and after (-0.007 day⁻¹) fire was also intermediate compared to other savannah streams (-0.0001 to -0.09 in Gonçalves-Júnior et al. (2007); Moretti et al. (2007); Rezende et al. (2018b, 2017, 2016)), and other tropical streams (-0.026 to -0.077 day⁻¹ in Abelho (2001); Gonçalves-Júnior et al., (2012b, 2016)). This may indicate that this stream savannah system has high resilience to the impacts of fire compared to other streams systems. Therefore, changes in *k* were not drastically altered in the short-term post-fire, regardless of litter quality.

Fungal biomass in the leaf litter of the studied stream (83 µg.g⁻¹ ergosterolAFDM ± SE) was lower than that reported for other streams in Brazilian Savannah (50–624 µg.g⁻¹; Gonçalves-Júnior et al. (2006); Gonçalves-Júnior et al. (2007); Rezende et al. (2014, 2017, 2016)), for tropical forest streams (4–306 µg.g⁻¹; Capps et al. (2011); Foucreau et al. (2013); Gonçalves-Júnior et al. (2016); MacKenzie et al. (2013)), and for temperate streams (200–1200 µg.g⁻¹; Abelho (2001); Danger et al. (2013); Feio et al. (2010)). On the other hand, fungal biomass differed significantly only between treatments. This result may indicate that: i) the invertebrate community, particularly scrapers controls fungal biomass in the leaf litter (Graça et al., 2016, 2015), mainly by biofilm

consumption (Rodríguez-Lozano et al., 2015); and ii) increased nutrients and water discharge post-fire may stimulate increased biomass of the hyphomycetes community (Pettit & Naiman, 2007). An increase in hyphomycetes biomass due to greater nutrients and water discharge was also reported for other Brazilian savannah stream systems despite lower breakdown rates (Rezende et al., 2017).

In conclusion, the contribution of allochthonous leaf breakdown to stream metabolism decreases post-fire due to higher autochthonous production, corroborating our first hypotheses. Thus, our results suggest a short-term post-fire change in the importance of autochthonous-allochthonous litter to Brazilian savannah stream metabolism (for more see also, Lau et al. (2008); Wagner et al. (2017)). Contrary to expectations, litter quality was of less importance than fire treatment, which refutes our third hypothesis, and indicates that leaf litter quality is equalized in stream ecosystems compounds it contains. Also, chemical characteristics of litter seem to have an important influence on leaf processing speed. On the other hand, scrapers were found to have an important influence on leaf breakdown rates, with their abundance decreasing post-fire. This result is in contrast to fungal biomass in breakdown process, indicating that post-fire may modify the relationships of relative importance within decomposer communities.

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