Differences in the decomposition of green and senescent leaves in streams of Reserva Florestal Adolpho Ducke (Amazonas, Brazil)

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ABSTRACT

Differences in the decomposition of green and senescent leaves in streams of Reserva Florestal Adolpho Ducke (Amazonas, Brazil). Leaves are considered the main energetic resource supply among all the allochthonous organic material available for the small shaded streams. However, their processing is limited by the physical and chemical characteristics of the leaves. Therefore, this research aimed to: i) evaluate the difference in decomposition coefficients between green and senescent leaves; ii) compare richness and density of aquatic invertebrates colonizing decomposing green and senescent leaves. Between November 2012 and January 2013, 12 leaf packages (6 senescent and 6 green) of 14 plant species were installed in 3 streams of the Reserva Florestal Adolpho Ducke (Manaus/AM - Brazil). After 15, 30 and 60 days the submerged packages were removed. The collected material was taken to the laboratory for analyzes of: aquatic invertebrates and leaves' mass remnants. Paired t-test was performed to verify if the decomposition coefficients (k) differed. ANCOVAs were performed to compare: the remaining mass (%), richness and density of aquatic invertebrates between leaf type over time. The green leaves presented higher leaf decomposition rates than in senescent ones. The leaf type influenced the average invertebrates densities. Therefore, green leaves were more susceptible to the colonization of aquatic invertebrates associated with the leaf decomposition process in small Amazonian streams.

KEY WORDS: aquatic invertebrates, community structure, organic substrates, igarapés, tropical region.

RESUMO

Diferenças na decomposição de folhas verdes e senescentes em riachos da Reserva Florestal Adolpho Ducke (Amazonas, Brasil). As folhas são consideradas a principal fonte de recurso energético entre toda a matéria orgânica alóctone disponibilizada para os pequenos riachos sombreados. Porém, seu processamento é limitado por características físicas e químicas das folhas. Assim, esta pesquisa objetivou: i) avaliar as diferenças nos coeficientes de decomposição entre folhas verdes e senescentes; ii) comparar a riqueza e a densidade de invertebrados aquáticos que colonizam folhas verdes e senescentes em decomposição. Entre novembro de 2012 a janeiro de 2013, foram instalados 12 bolsas de folhas (6 senescentes e 6 verdes) de 14 espécies vegetais em 3 riachos da Reserva Florestal Adolpho Ducke (Manaus/AM – Brasil). Após 15, 30 e 60 dias houve a retirada das bolsas submersas. O material coletado foi levado ao laboratório para as análises de: invertebrados aquáticos e massa remanescentes de folhas. Teste-t pareado foi realizado para verificar se havia diferenças entre os coeficientes de decomposição (k). ANCOVAs foram realizadas para comparar: a massa remanescente (%), riqueza e densidade de invertebrados aquáticos entre os tipos de folha ao longo do tempo. As folhas verdes apresentaram maiores taxas de decomposição foliar do que em senescentes. O tipo da folha influenciou as densidades médias de invertebrados. Portanto, folhas verdes foram mais susceptíveis a colonização de invertebrados aquáticos associados ao processo de decomposição foliar em riachos amazônicos.

PALAVRAS CHAVE: invertebrados aquáticos, estrutura de comunidade, substratos orgânicos, igarapés, região tropical

INTRODUCTION

Leaves are considered the main energetic resource supply among all the allochthonous organic material available for the small shaded streams (França *et al*. 2009). However, the processing of this leaf material can be limited by the physical and chemical characteristics of the leaves that enter the streams (Rincón and Santelloco 2009; Bruder *et al*. 2014). For instance, leaves with high structural compounds concentrations (lignin and cellulose) may remain in the aquatic system for longer time (Moretti *et al*. 2007a, b), since these characteristics hinder the processing by the aquatic decomposing community (Ardón and Pringle 2008; Moretti *et al*. 2009).

The processing of leaf material involves the participation of two groups of organisms: the decomposers (bacteria and fungi) and the detritivores (animals that consume dead matter) (Townsend *et al*. 2006; Graça *et al*. 2001a,b; 2015). Bacteria and fungi are responsible for conditioning of plant material incorporated into the aquatic system (Gonçalves *et al*. 2006a, b; Alvim *et al*. 2015). Conditioning is the stage of leaf decomposition process in which microorganisms act on dead organic matter, making it more palatable to the detritivore community, especially aquatic invertebrates (Graça 2001; Gonçalves *et al*. 2014).

Aquatic invertebrates, especially the shredders, are responsible for transforming coarse particulate organic matter into fine particulate organic matter (Abelho 2001; Graça *et al*. 2015), acting directly on the leaf decomposition process (Webster and Benfield 1986; Gessner *et al*. 1999). The attractiveness of foliar debris to aquatic invertebrates has been associated with its chemical and physical composition, level of decomposition and microbial conditioning of the leaves (Abelho 2001; Graça *et al*. 2001a; Gonçalves *et al*. 2014; Alvim *et al*. 2015; Graça *et al*. 2015). In addition, the exposure time of the leaves can also be considered an important factor to determine the taxonomic composition of aquatic invertebrates involved in their decomposition (Ligeiro *et al*. 2010).

Most leaf decomposition studies are based on experiments using senescent leaves to represent the natural processes of leaf decomposition (see Gonçalves *et al*. 2014). The process of senescence consists of a series of biochemical event which results in the breakdown of biochemical compounds, culminating in the death of parts of the plant, such as leaves or the plant itself (Diaz *et al*. 2008; Hollmann *et al*. 2014; Jyothsna and Murthy 2016; Clément *et al*. 2017). Leaf senescence allows the translocation of nutrients such as Nitrogen (Diaz *et al*. 2008; Hollmann *et al*. 2014) from the senescent organs to other, growing plant organs, such as seeds (Clément *et al*. 2017). Therefore, senescence is considered the final stage of development for leaves. According to Peoples and Dalling (1988), up to 70% of the leaf nitrogen can be translocated from senescent organs to other parts of the plant. Thus, senescent leaves are considered less nutritious than green leaves (Kochi and Yanai 2006).

Some research on foliar decomposition has been developed with green leaves (Landeiro *et al*. 2008; Ferreira *et al*. 2012; Martins *et al*. 2015; Gonçalves *et al*. 2017), sometimes with the justification that green leaves represent an important energy source (Lopes *et al*. 2015), or due to the unfeasibility of collecting senescent leaves in some ecosystems. Thus, the use of green leaves almost always implies greater nutritional availability (Bastian *et al*. 2007) that allows for greater attractiveness to organisms associated with their decomposition, and, therefore, it assumes that their rates of decomposition are greater than with senescent leaves.

Therefore, this research aimed to: i. evaluate the difference in decomposition coefficients between green and senescent leaves; ii. compare richness and density of aquatic invertebrates colonizing decomposing green and senescent leaves.

MATERIAL AND METHODS

Study area

Sampling was conducted between November 2012 and January 2013 in three first- or second -order streams (Strahler 1952) at Reserva Florestal Adolpho Ducke (RFAD) (Figure 1). RFAD is a 10,000ha (10km x 10km) tropical forest environmental protection area located North of the city of Manaus, state of Amazonas, Brazil (02°55' – 03°01' S; 59°53' – 59°59' W). This area is characterized by the humid tropical climate with two well-defined seasons (Köppen climate classification): a dry
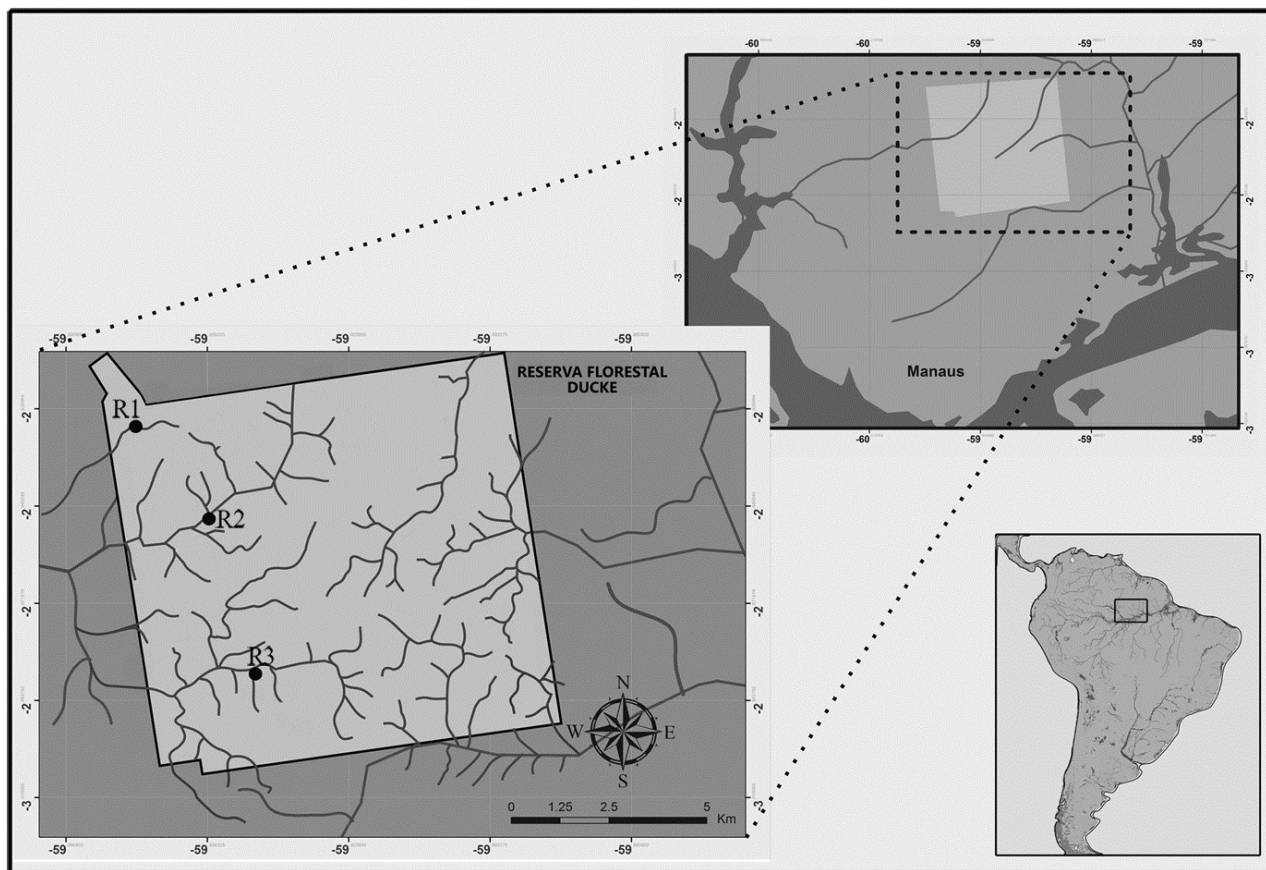
Figure 1. Localization of the three selected streams to carry out a leaf decomposition experiment located at Reserva Florestal Adolpho Ducke, Manaus (AM). Sampling was conducted between November 2012 and January 2013.

one, from June to November, and a wet one, from December to May. The annual average temperature is 26.7°C and the monthly average relative humidity is above 80% (Marques-Filho and Dallarosa 2000).

The studied streams present a predominantly sandy bed associated with accumulation of leaf litter or other plant material (trunks, branches and fruits) (Rezende 2007; Espírito-Santo *et al*. 2009); acidic pH between 4.19 – 4.50 (average 4.36 ± 0.11); low average electrical conductivity (11.18 ± 2.97µS cm^{-1}); average water temperature at approximately 25.09 ± 0.37°C and water dissolved oxygen between 3.86 – 7.39 mg l^{-1} (average 4.98 ± 1.09mg l^{-1}). Average stream width was 68 ± 0.22cm, average depth was 7 ± 0.03cm and average speed, 0.16 ± 0.07m s^{-1}.

Experimental procedure

Fourteen plant species were selected for this study: *Croton lanjouwensis* Jabl. (Euphorbiaceae), *Hevea brasiliensis* Müll. Arg. (Euphorbiaceae), *Dipteryx odorata* (Aubl.) Willd. (Fabaceae), *Eperua glabriflora* (Ducke) R. S. Cowan (Fabaceae), *Ficus* sp. (Moraceae), *Helicostylis tomentosa* (Poepp. & Endl.) Rusby (Moraceae), *Carapa guianensis* Aubl. (Meliaceae), *Cecropia hololeuca* Miq. (Cecropiaceae), *Clusia* sp. (Clusiaceae), *Davilla rugosa* Poir. (Dilleniaceae), *Eugenia stipitata* McVaugh (Myrtaceae), *Lecythis pisonis* Cambess (Lecythidaceae), *Licania* sp. (Chrysobalanaceae) and *Ocotea nigrescens* Vicent. (Lauraceae). Species were selected based on their occurrence among riparian vegetation in the studied streams and availability of their leaves.

Both senescent and green leaves (removed before natural abscission) were collected and taken to laboratory, where leaves were further selected, discarding those that presented foliar tissue damage or established microorganism colonies.

Leaves were then stored in hollow plastic containers (standard, 60 x 40cm) to dry in controlled conditions (~72h, 18°C).

A total of 504 leaf samples were used in this

study, with 18 litter bags for each plant species and for each leaf state (green leaf or senescent leaf). Litter bags were made of plastic mesh measuring 10 x 20cm, with a 1cm² opening between knots, containing approximately 2.13g (± 0.33g) of leaf litter.

All litter bags were submerged on the same date and secured by nylon cords attached by rods to the bed of the streams, maintaining a 10cm distance between bags. Six packets of leaves of each plant species and each leaf state (senescent and green) were installed in each stream.

Removal and processing of leaf litter bags

After 15, 30 and 60 days of incubation, 4 litter bags were collected from each stream for each plant species, being 2 litter bags of senescent leaves and 2 of green leaves. The removed bags were immediately moved to individual plastic bags and transported in iceboxes to the Laboratório de Citotaxonomia e Insetos Aquáticos at Instituto Nacional de Pesquisas da Amazônia.

The leaves from each bag were carefully washed with distilled water in the laboratory over a sieve with a mesh aperture of 120µm. A set of five leaf discs with a diameter of 1.2cm was taken from each bag to estimate the ash-free dry mass (AFDM) (Graça et al. 2005). However, it was not possible to perform this procedure for all litter bags, because due to the advanced state of leaf decomposition there was not enough plant material remaining in some bags to perform the analyses.

Leaf decomposition

The percentage of remaining mass was estimated from the starting weight and final weight of the remaining material. The decomposition coefficient (k) of the litter bags was obtained through a negative exponential model of the litter bag weight percentage over time ($W_t = W_0 . e^{-kt}$, where W_t = final weight; W_0 = starting weight; $-k$ = decay rate and t = time). Subsequently, the decomposition coefficients obtained were used to establish a regional classification for decomposition velocities.

AFDM estimates for each species were obtained from a set of leaf discs dried in a bacteriological stove (50°C for 72h), weighted with a precision analytical balance (0.0001g) and calcined in a muffle oven (500°C for 4h).

After calcination, the remaining material was reweighed in a precision analytical balance and the AFDM values were extrapolated for the remaining litter mass (see Gonçalves et al. 2014).

Aquatic invertebrates

All aquatic invertebrates retained in the sieve after the leaves were washed were separated into plastic vials with ethyl alcohol at 80% and properly labeled. Subsequently, aquatic invertebrates were screened, quantified and identified at family level using stereoscopic microscopes and taxonomic keys by Pes et al. (2005); Pereira et al. (2007); Hamada and Ferreira-Keppler (2012) and Hamada et al. (2014). Examined specimens are deposited in the Invertebrate Collection of the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Amazonas, Brazil.

Data analysis

A paired t-test was performed to test whether the coefficients of decomposition (k) presented significant differences between the studied leaf states (senescent vs. green). To compare the remaining mass (%) between senescent and green leaves, time and the interaction between these two factors, Covariance analyses (ANCOVA) were performed considering time as covariate.

Covariance analyses (ANCOVA) were also used to compare biotic variables (richness and density) of aquatic invertebrates between leaf states over time (covariate). The interaction between the predictive variables (leaf state vs. incubation time) relative to response variables. Data were log-transformed for analysis when necessary ($\log_{(x+1)}$) (Zar 1996).

Statistical analyses consider the sample mean by type of detritus and by incubation time for each plant species. All analyses considered a p = 0.05 significance level and were performed using R software (R Core Team 2013).

RESULTS

Remaining mass and leaf decomposition coefficient

The values of the decomposition coefficient (k) of the senescent leaves were significantly

lower than the values found for the green leaves (paired T test: t = − 4.2107; DF = 13; p = 0.001) (Table 1). Thus, approximately 78 days of incubation would be necessary for the senescent leaves decay to reach 50% of mass decomposition, while for green leaves the 60 days of incubation were sufficient for this to occur. At 60 days of incubation, the remaining dry weight percentage ranged from 43.7 − 79.4% for senescent leaves and 15.5 − 72.7% for green leaves, with mean values of 62.5% and 42.9%, respectively (Figure 2). The percentage of remaining dry weight of leaf litter was significantly different for senescent and green leaves (ANCOVA: F = 31.66; DF =

Table 1. Estimated decomposition coefficients for plant species used in the leaf decomposition experiment in three streams of the Reserva Florestal Adolpho Ducke, Manaus (AM).

Leaf species	Leaf state	
	Senescent (k day^{-1})	Green (k day^{-1})
Clusia sp.	0.005	0.009
Eugenia stipitata	0.010	0.013
Carapa guianensis	0.008	0.018
Dipteryx odorata	0.009	0.022
Hevea brasiliensis	0.014	0.024
Ficus sp.	0.010	0.020
Cecropia hololeuca	0.007	0.021
Helicostylis tomentosa	0.006	0.032
Croton lanjouwensis	0.009	0.008
Ocotea nigrescens	0.013	0.016
Eperua glabriflora	0.004	0.005
Licania sp.	0.014	0.016
Davilla rugosa	0.009	0.015
Lecythis pisonis	0.006	0.015
Mean and standard errors	0.009 ± 0.003	0.017 ± 0.007

1, p < 0.05) and for different incubation times (ANCOVA: F = 27.22; DF = 2, p < 0.05). However, no significant difference was found for the interaction of leaf state and time (ANCOVA: F = 1.21; DF = 2; p = 0.30) (Table 2).
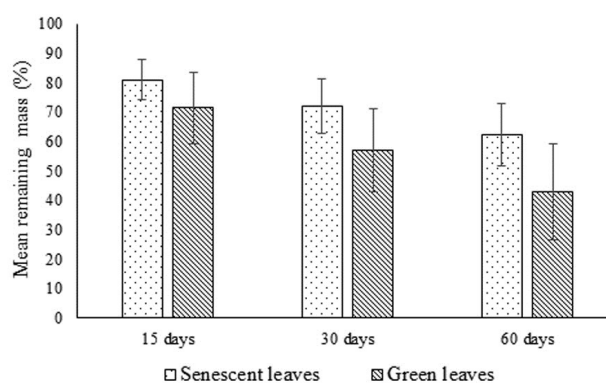

Figure 2. Mean percentage (columns) and standard errors (vertical bars) of the remaining mass - senescent and green - throughout the days of immersion in an experiment carried out in three streams of the Reserva Floresta Adolpho Ducke, Manaus (AM). Sampling was conducted between November 2012 and January 2013.

Aquatic invertebrates community

A total of 18,617 aquatic invertebrate individuals were collected, distributed in 45 taxa, associated to leaf decomposition. Average taxon richness did not differ significantly between the types of debris studied (ANCOVA: F = 0.05; DF = 1; p = 0.82). However, there were significant differences relative to incubation time (ANCOVA: F = 72.27; DF = 2; p < 0.05). Average densities exhibited a constant increase over decomposition time, for both state of leaves. These values presented significant differences between types of leaf (ANCOVA: F = 491.67; DF = 1; p < 0.05) and over sampling time (ANCOVA: F = 136.71; DF = 2; p < 0.05) (Table 2).
For all sampling events, green leaves presented higher average mean densities (Figure 3). At 15 days of incubation, green leaves presented 48.1 ± 21.7 ind. g^{-1} AFDM, reaching up to 104.6 ± 80.5 ind. g^{-1} AFDM at 60 days of incubation. For senescent leaves, these values were 18.2 ± 9.8 ind. g^{-1} AFDM and 45.6 ± 21.6 ind. g^{-1} AFDM, respectively (Figure 3).The composition of the community was similar among the leaf state studied. For example, in both cases the predominant taxa were Chironomidae (Diptera, Insecta), Leptohyphidae (Ephemeroptera, Insecta) and Hydroptilidae (Trichoptera, Insecta) (Figure 4 and 5).
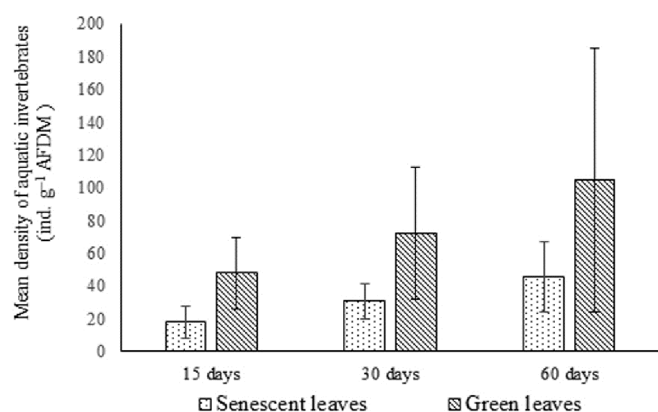
Figure 3. Mean density of aquatic invertebrates (columns) and standard errors (vertical bars) collected in the leaves analyzed throughout the days of immersion in an experiment carried out in three streams of the Reserva Floresta Adolpho Ducke, Manaus (AM). Sampling was conducted between November 2012 and January 2013.

DISCUSSION

Remaining mass and leaf decomposition coefficient

Green leaves presented higher decomposition rates than senescent leaves. Both leaf state presented average decomposition coefficients classified as "intermediate" according to the classification proposed by Gonçalves *et al*. (2014). However, the k value for green leaves was approximately twice as high as the value for senescent leaves, so that while green leaves lost over 50% of biomass in 60 days of debris incubation, senescent leaves would require more time. This indicates that changes in the composition of riparian vegetation, which will affect the quality of the leaf litter supplied to the streams, can impact the leaf decomposition process in

Table 2. Analysis of Covariance (ANCOVA) used to evaluate if the percentage of remaining mass and the aquatic invertebrates community (richness and density) showed differences between leaf state (green or senescent), incubation times (15, 30 and 60 days) and the interaction of these two factors in a leaf decomposition experiment in three streams of the Reserva Florestal Adolpho Ducke, Manaus (AM).

| Response variables	Predictive variables	DF	Sum of squares	Mean of squares	F	p
% Remaining mass	Leaf state	1	4524.5	4524.5	301.31	**<0.05**
	Time	2	7117.90	3559.00	237003.00	**<0.05**
	Leaf state x Time	2	445.40	222.70	14832.00	0.23
	Residuals	78	11712.90	150.20		
Aquatics invertebrate richness	Leaf state	1	0.00	0.00	0.05	0.82
	Time	2	0.55	0.27	72.27	**<0.05**
	Leaf state x Time	2	0.15	0.07	19.67	0.15
	Residuals	78	295.33	0.04		
Aquatics invertebrate density	Leaf state	1	131.63	131.63	491.67	**<0.05**
	Time	2	72.93	36.46	136.20	**<0.05**
	Leaf state x Time	2	10.53	0.53	19.67	0.15
	Residuals	78	208.82	0.27		
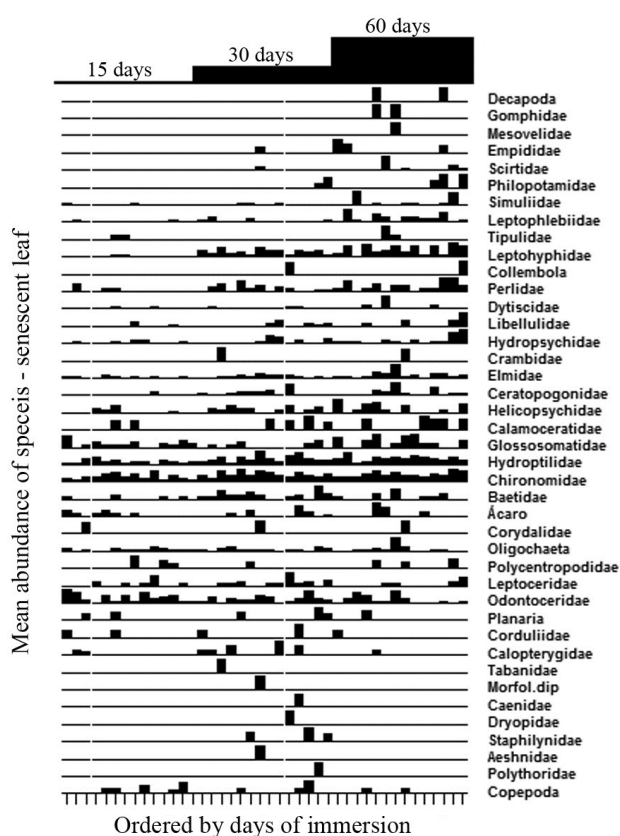
Figure 4. Mean abundance of aquatic invertebrates found in senescent leaves, ordered by the number of days of incubation in leaf decomposition experiment carried out in three streams of the Reserva Floresta Adolpho Ducke, Manaus (AM). Taxons were ordered on the y-axis. Sampling was conducted between November 2012 and January 2013.
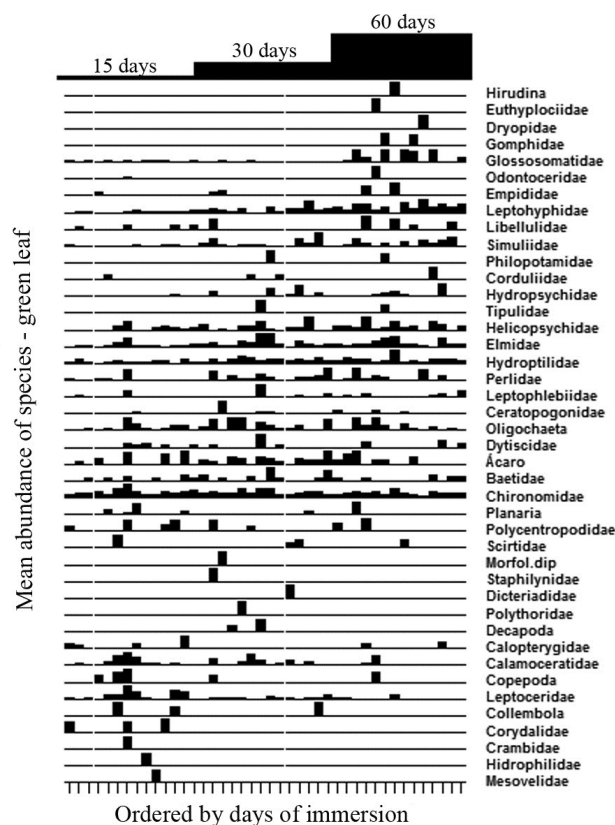
Figure 5. Mean abundance of aquatic invertebrates found in green leaves, ordered by the number of days of incubation in leaf decomposition experiment carried out in three streams of the Reserva Floresta Adolpho Ducke, Manaus (AM). Taxons were ordered on the y-axis. Sampling was conducted between November 2012 and January 2013.

these aquatic systems since the physical and chemical characteristics of the leaves are determinant of their decomposition rates (Biasi *et al.* 2016; Gonçalves *et al.* 2017).

Aquatic invertebrates

Aquatic invertebrates play an important role in the process of foliar decomposition, fragmenting and/or reducing coarse particulate matter into smaller parts (Graça 2001). In the present study, richness of invertebrate communities were similar for green and senescent leaves. Thus, although taxonomic richness is an important factor in community ecology, it may not be a good predictor for leaf decomposition studies, since taxonomic richness is not influenced by the nutritional quality of the leaf litter, due to the adaptation that different groups of invertebrates possess to explore different resources (König *et al*. 2014).

The predominance of Chironomidae on green and senescent leaves agrees with other studies of leaf decomposition in streams in the Brazilian Amazon forest (e.g. Landeiro *et al.* 2008; Landeiro *et al.* 2010; Martins *et al*. 2015). These larvaes were found colonizing all the leaves studied in this study. These organisms are recognized for having generalist feeding habits (Roque and Trivinho-Strixino 2001; Trivinho-Strixino and Strixino 1999), and are important in the colonization of different state of foliar debris, regardless of their quality (Moretti *et al.* 2007a,b; Biasi *et al.* 2013). It is possible that such trophic behavior favored their plastic ability as colonizers, characterizing them as important biological agents in leaf decomposition. Moreover, they may act as essential agents in early stages of decomposition, when few organisms are able to act on submerged plant matter.

The data obtained showed that the mean

densities of aquatic invertebrates were influenced by the leaf state and the time of removal from water. The patterns found for mean density of invertebrates were similar to those recorded in other studies, where the highest densities are found associated with latest sampling times (Kochi and Yanai 2006; Ligeiro *et al*. 2010; König *et al*. 2014). Higher invertebrate densities found in the longest incubation times may be a result of the aggregation of individuals over smaller amounts of leaves available (König *et al*. 2014).

In our study, in the last sampling event, much of the incubated debris had already been degraded both in green and senescent leaf samples. Thus, at that time, the lower availability of "leaf debris area" for colonization possibly led to the aggregation of individuals over available matter, thus increasing their densities. Furthermore, leaves in further stages of decomposition are likely a better substrate once they have undergone chemical and microbial conditioning, and, therefore, become more suitable for invertebrate colonization (Abelho 2001; Graça 2001).

CONCLUSION

In the beds of the small streams of the Amazon region, it is often possible to observe green leaves available, even though they are present in smaller quantities relative to senescent leaves. In our study, leaf decomposition rates were higher in green leaves than in senescent leaves. Aquatic invertebrate richness was not influenced by whether leaves were green or senescent. However, leaf type influenced the mean density of aquatic invertebrates.The higher density of organisms in the green leaves may be due to the chemical and physical characteristics that favor the colonization of these organisms. However, we suggest that larger studies are carried out to evaluate how the physical and chemical characteristics of the leaves and the fungal biomass are conduct throughout the process of leaf decomposition among the leaf types studied here.

ACKNOWLEDGEMENTS

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