Journal of Tropical Ecology (2007) **23**:329–335.
doi:10.1017/S0266467406003956 Printed in the United Kingdom

Litterfall production and fluvial export in headwater catchments of the southern Amazon

Evandro Carlos Selva*, Eduardo Guimarães Couto*, Mark S. Johnson†[1] and Johannes Lehmann†

* Departamento de Solos, Universidade Federal de Mato Grosso, 78060-900 Cuiabá, MT, Brazil
† Department of Crop and Soil Sciences, Cornell University, Ithaca, NY 14850, USA
(*Accepted 6 December 2006*)

Abstract: Resolving the carbon (C) balance in the Amazonian forest depends on an improved quantification of production and losses of particulate C from forested landscapes via stream export. The main goal of this work was to quantify litterfall, the lateral movement of litter, and the export of coarse organic particulate matter (>2 mm) in four small watersheds (1–2 ha) under native forest in southern Amazonia near Juruena, Mato Grosso, Brazil (10°25′S, 58°46′W). Mean litterfall production was 11.8 Mg ha^{-1} y^{-1} (5.7 Mg C ha^{-1} y^{-1}). Litterfall showed strong seasonality, with the highest deposition in the driest months of the year. About two times more C per month was deposited on the forest floor during the 6-mo dry season (0.65 Mg C ha^{-1} mo^{-1}) compared with the rainy season (0.3 Mg C ha^{-1} mo^{-1}). The measured C concentration of the litterfall samples was significantly greater in the dry season than in the rainy season (49% vs. 46%). The lateral movement of litter increased from the plateau (upper landscape position) towards the riparian zone. However, the trend in C concentration of laterally transported litter samples was the opposite, being highest on the plateau (44%) and lowest in the riparian zone (42%). Stream-water exports of particulate C were positively correlated with streamflow, increasing in the rainiest months. The export of particulate C in streamflow was found to be very small (less than 1%) in relation to the amount of litterfall produced.

Key Words: Amazon basin, Brazil, lateral movement, litterfall, run-off, small watersheds, streams, tropical forest

INTRODUCTION

Terrestrial litterfall is thought to be a major source of CO_2 lost to the atmosphere from tropical rivers and wetlands through evasion (e.g. outgassing) (Richey *et al.* 2002). Evasion of CO_2 from tropical rivers has been shown to be a significant term in the global carbon budget, equivalent to nearly 10^{15} g C y^{-1} (Grace & Malhi 2002, Richey *et al.* 2002). Isotopic evidence suggests that much of the CO_2 that outgases from Amazonian rivers is originally fixed in the terrestrial biosphere, yet cycles back to the atmosphere in less than a decade (Mayorga *et al.* 2005) after escaping decomposition across the terrestrial landscape (Cole & Caraco 2001). Richey *et al.* (2002) used terrestrial litterfall rates to estimate that 47% of the terrestrially derived C that is respired in the Amazon River system originates as terrestrial litterfall. However, no empirical data for litter transfer from terrestrial to aquatic systems are available for terra firme ecosystems in the Amazon to assess the contribution of litterfall in headwater catchments to downstream transport and stream respiration.

Terrestrial litter enters the aquatic environment with overland flow, by wind, by streambank erosion, as well as by direct litterfall from overhanging riparian vegetation (Benfield 1997, McClain & Elsenbeer 2001, McClain & Richey 1996, Melack & Forsberg 2001, Richey *et al.* 2002). The entry of litter materials to streams is controlled by factors such as vegetation, topography, soil structure and composition, lithology and precipitation characteristics (e.g. frequency and intensity) (Cummins *et al.* 1983, Dolloff & Webster 2000, Hall *et al.* 2000, Wallace *et al.* 1995). The transport pathways by which litter is mobilized, its travel time, and the chemical composition and decomposition characteristics of the source litter material influence the bioavailability of the material that is ultimately delivered to streams (McClain & Elsenbeer 2001).

The Juruena watershed study area in the Southern Amazon provided an opportunity to investigate litter production, transport and export in four adjacent forested headwater catchments. We were interested in

[1] Corresponding author. Email: msj8@cornell.edu

determining the amount of terrestrial litterfall at the hillslope and headwater scales in terra firme catchments that is mobilized downstream to larger order rivers in the Amazon, where it is subjected to further decomposition and loss via CO_2 outgassing (Mayorga *et al.* 2005, Richey *et al.* 2002). As such, the objectives of this study were to: (1) determine the export of coarse particulate organic matter (CPOM) by first-order streams in relation to litterfall production of terrestrial systems and precipitation, and (2) investigate litter transport over the soil surface as a function of slope. We hypothesized that litter transport would be greater on steeper slopes, and that litter export by headwater streams would exhibit the same seasonal pattern as litterfall production.

METHODS

Study site

The present study was conducted in four headwater catchments from September 2003–August 2004. The study catchments each contain a toposequence of landscape positions from a gently sloping upper plateau to a steep riparian hillslope, and are representative of terra firme catchments in the region (rather than floodplain-dominated low-gradient catchments). The watersheds (*c.* 1–2 ha each) comprise a subcatchment of the Juruena River, in the southern portion of the Amazon basin (10°25′S, 58°46′W). The watersheds are under primary forest (terra firme), with a mixed stand of hardwood and palm species in the riparian zone. The mean annual temperature is 24 °C, with minimum and maximum temperatures during the study period of 16 °C and 32 °C, respectively. Rainfall during the study period totalled 2379 mm in a unimodal distribution, with 70% of the precipitation occurring during the rainy season (November–April). Precipitation in the study year was close to the annual mean 2585 mm ± 460 mm (mean ± 1 SD for 15 y of data in Cotriguaçú, 50 km from the study site) (A. Castanha, pers. comm.).

The soils of the watersheds are classified as Oxisols and Ultisols, respectively in U.S. Soil Taxonomy, with Ultisols occupying the majority of the landscape. Both soils are of low fertility with less than 50% base saturation in the upper 20 cm of soil, and have medium texture (15–35% clay content increasing with depth) (Johnson *et al.* 2006, Novaes Filho *et al.* in press).

Litterfall collection

Sixteen litterfall collectors (1 m^2 collection area) were constructed of a plastic mesh with 2 mm openings. These were installed 50 cm above the forest floor at four randomized locations in each of the four watersheds. Litterfall was separated into three fractions: leaves, branches > 1 cm, and miscellaneous. The miscellaneous fraction contained twigs, fruits and flowers. Litterfall was collected at least every 15 d in the rainy period, and at least every month in the dry period. Throughfall was determined from four below-canopy rain gauges as described in Johnson *et al.* (2006).

Lateral litter movement collectors

Litter movement collectors were designed to trap litter transported along the forest floor, regardless of mechanism of movement. The collectors were made in the shape of a box, with 2-mm mesh on five sides and the sixth side open to permit entry of litter materials. The opening (1.2 m wide by 0.33 m high) was oriented upslope, and the bottom of the box (1.2 m wide by 0.33 m deep) was fixed to the ground with stakes. Following a topographic survey, each watershed was subdivided into three landscape components based on slope: the upper plateau (PL) (0–20% slope), upper hillslope (UH) (20–40%), and steep riparian hillslope (RH) (>40% slope). Five collectors were then located randomly within each of the three landscape components in the four watersheds, for a total of 60 collectors. The distance between collectors was typically 5–10 m, and the collection intervals coincided with the litterfall collections. Lateral litter movement is reported as g C m^{-1}.

In-stream coarse particulate organic matter collectors

In order to capture coarse particulate organic matter (CPOM) transported by stream water and exported from the watersheds, weir traps were installed on the downstream side of V-notch weirs at each of the watershed outlets (Johnson *et al.* 2006). These weir trap collectors were made from the same plastic mesh as the other collectors, and were installed such that all coarse particulate matter exported from the watersheds was retained in the trap and was removed during routine sample collection. The traps were constructed in the shape of a cube (1 m on all sides), with the bottom opening to the trap located below the base of the V-notch so as to not interfere with the free discharge of water over the weir.

Samples from the weir traps were collected every 15 d. Of these samples, 16 were analysed for particle size distribution following air drying in the laboratory, and were evenly distributed between the two seasons.

Sample preparation and analysis

Litterfall, laterally transported litter and stream flow CPOM exports were dried to constant mass (70 °C) and ground on a Wiley mill. Samples were analysed in the Limnology Laboratory of the Federal University of Mato Grosso for C concentration on a total carbon analyser (Multi N/C, Analytik Jena, Jena, Germany) with an in-line furnace for analysis of solid samples (Eltra HTF-540, Neuss, Germany). Ground samples were introduced into the 1300 °C furnace where all carbonaceous materials were converted to CO_2, which was immediately analysed by infrared gas analysis (Buurman *et al.* 1996).

Particle size distribution was determined for stream-water CPOM samples by sieving samples for 5 min using an automated sieve shaker (2 cycles per second). Size classes were based on available sieve sizes: large fraction (>7.93 mm), medium fraction (2.38–7.93 mm), and small fraction (<2.38 mm).

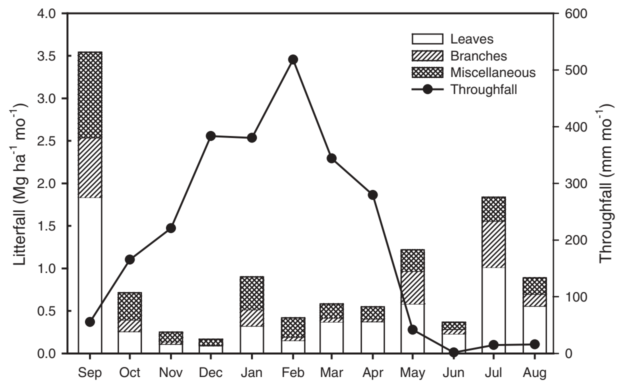

Figure 1. Mean monthly litterfall production in headwater catchments in the southern Amazon on a dry-matter basis, 2003–2004. The three fractions comprise total litterfall. Throughfall is mean monthly data from four collectors within study area (throughfall data from Johnson *et al.* 2006).

RESULTS

Litterfall production and litterfall C

The mean litterfall for the 1-y period of study was 11.8 Mg ha^{-1} (Table 1), and was not significantly different between watersheds ($P = 0.64$, one-way ANOVA). Litterfall rates during the dry season were considerably higher than those of the rainy season (8.0 vs. 3.8 Mg ha^{-1}), with the greatest litterfall production occurring in the driest months (Figure 1). Litterfall deposition rates of the various fractions covaried over the course of the study (Figure 1), with peak production during the months of May, July and September. The dry season months of July through September accounted for 58% of the total litterfall for the study year, while litterfall during the month of September was 31% of the annual total (Figure 1). January showed peak rainy season litterfall rates.

The leaf fraction represented 50% of the total litterfall produced during the year, thus comprising the largest component of litterfall (Table 1), followed by the miscellaneous fraction (30% of total) and the branch fraction (20% of total). The branch fraction was the most temporally variable litterfall component, comprising from 17% (May) to 30% (September) of total litterfall.

The C concentration of total litterfall in the four watersheds had a mean value of 48%, with C concentration highest for the branch fraction (52%), followed by miscellaneous (48%) and leaf (47%) fractions (Table 1). Considering the C concentration of litterfall over the course of the year, the net deposition to the forest floor of C via litterfall was 5.7 Mg C ha^{-1} y^{-1}.

The dry-season litterfall C concentration (48%) was slightly higher than the rainy-season litterfall C concentration (46%). In proportional terms, two times more C was deposited as litterfall in the 6 months of the dry season than in the 6 months of the rainy season: 3.9 and 1.8 Mg ha^{-1} y^{-1} respectively (Table 1).

Table 1. Production, C concentration and C flux in terrestrial litterfall in headwater watersheds in the southern Amazon. Values presented are mean ± 1 SE for four watersheds for September 2003–September 2004, with seasons divided between wet (November–April) and dry (May–October).

Fraction	Period	Litterfall (Mg ha^{-1})	Carbon concentration (%C)	Litterfall C (Mg C ha^{-1})
Total litterfall	Annual	11.8 ± 0.7	48.2 ± 0.5	5.7 ± 0.3
	Dry season	8.0 ± 0.4	48.9 ± 1.1	3.9 ± 0.2
	Wet season	3.8 ± 0.3	46.4 ± 1.0	1.8 ± 0.2
Leaves	Annual	5.9 ± 0.2	46.8 ± 0.3	2.8 ± 0.1
	Dry season	4.4 ± 0.2	47.4 ± 0.4	2.1 ± 0.1
	Wet season	1.5 ± 0.1	45.0 ± 0.3	0.7 ± 0.1
Branches	Annual	2.4 ± 0.3	52.2 ± 4.6	1.3 ± 0.2
	Dry season	1.6 ± 0.3	53.0 ± 5.0	0.9 ± 0.2
	Wet season	0.8 ± 0.2	47.5 ± 0.5	0.4 ± 0.1
Miscellaneous	Annual	3.5 ± 0.2	47.7 ± 1.1	1.7 ± 0.1
	Dry season	2.0 ± 0.1	47.8 ± 0.7	1.0 ± 0.0
	Wet season	1.5 ± 0.2	47.3 ± 2.1	0.7 ± 0.1

Lateral movement of litter

Litter that moved laterally over the soil surface was monitored for 1 y in three landscape positions in each of the four watersheds. No significant differences in litter movement were found among watersheds for comparable landscape positions.

Both the C concentration and the total lateral transport of litter-C determined from the lateral collectors varied significantly in relation to landscape position. The amount of transported litter was found to increase from upper to

Table 2. Annual lateral litter movement at different landscape positions in headwater catchments of the southern Amazon. Values presented are mean ± 1 SE for four watersheds for September 2003–September 2004, with seasons divided between wet (November–April) and dry (May–October).

Period	Landscape position	Litter ($g\,DM\,m^{-1}$)	Carbon concentration (%C)	Litter C ($g\,C\,m^{-1}$)
Annual (12 mo)	Plateau	227 ± 13.5	44.0 ± 0.3	102 ± 3.7
	Upper hillslope	403 ± 133	42.9 ± 1.0	152 ± 40.8
	Riparian hillslope	404 ± 116	42.0 ± 0.8	170 ± 49.0
Dry season (6 mo)	Plateau	141 ± 15.2	45.0 ± 0.4	67.0 ± 4.7
	Upper hillslope	176 ± 44.3	44.1 ± 0.5	78.1 ± 19.8
	Riparian hillslope	254 ± 73.2	43.7 ± 1.0	111 ± 33.4
Wet season (6 mo)	Plateau	86.2 ± 6.4	43.0 ± 0.5	34.8 ± 1.6
	Upper hillslope	227 ± 114	41.6 ± 1.4	74.0 ± 28.1
	Riparian hillslope	150 ± 44.9	39.9 ± 1.3	58.5 ± 16.8

lower landscape positions, while the C concentration of transported litter decreased from upper to lower landscape positions (Table 2).

In addition, the lateral movement of litter-C was strongly seasonal, and was found to be highest during the dry season (May to October). This seasonality was exhibited in all landscape positions (Table 2). Among landscape positions, the mean litter-C transported laterally was highest on the upper hillslope (UH) during the 6-mo rainy season (74.0 $g\,C\,m^{-1}$), while during the 6-mo dry season it was highest on the steep riparian hillslope (RH) (111.2 $g\,C\,m^{-1}$).

We found litter that was transported laterally to have a higher C concentration during the dry season than during the rainy season. Further, the RH litter material collected in the riparian areas was found to have a lower C concentration than in the other landscape positions, indicating a more degraded litter material was transported in the riparian zone than in the upper landscape positions.

Litter export as CPOM

Coarse particulate organic matter exported from the headwater catchments by stream flow totalled 3.6 kg CPOM $ha^{-1}\,y^{-1}$ (Table 3). The mean C concentration of CPOM during the period of study was 43%. The CPOM exports were positively related to both discharge

Table 3. Coarse particulate organic matter export (CPOM), organic C concentration and coarse particulate organic C (CPOC) exports from headwater catchments in the southern Amazon. Values presented are mean ± 1 SE for four watersheds for September 2003–September 2004, with seasons divided between wet (November–April) and dry (May–October).

Period	CPOM ($kg\,ha^{-1}\,y^{-1}$)	Carbon concentration (%C)	CPOC ($kg\,ha^{-1}\,y^{-1}$)
Annual	3.59 ± 0.99	42.7 ± 1.0	1.52 ± 0.41
Dry season	0.59 ± 0.08	42.9 ± 0.8	0.25 ± 0.04
Wet season	3.01 ± 1.04	42.6 ± 1.2	1.26 ± 0.44

($r^2 = 0.52$; $P = 0.008$, least-squares linear regression) and throughfall ($r^2 = 0.3$; $P = 0.07$).

Based on the C concentration determined for each CPOM sample collected from the weir traps, it was possible to calculate C exports as CPOM from the four watersheds. Coarse particulate organic carbon fluxes (carbon export as CPOM (>2 mm)) totalled 1.5 ± 0.4 kg C $ha^{-1}\,y^{-1}$, (mean ± 1 SE). In view of total organic C exported by streamwater of these catchments (CPOC in addition to dissolved organic C and particulate organic C < 2 mm reported by Johnson *et al.* 2006), CPOC represented only 3.5% of the total organic C exports.

CPOC exports showed a high degree of temporal variability over the course of the study (Figure 2). Eighty-three per cent of CPOC exports occurred during the rainy season (Table 3). In addition, exported CPOM was also more physically degraded during the rainy season, during which the smallest size fraction represented 39% of the total CPOM exports. In contrast, the largest size fraction contained 85% of the total CPOM exported during the dry season (Table 4).

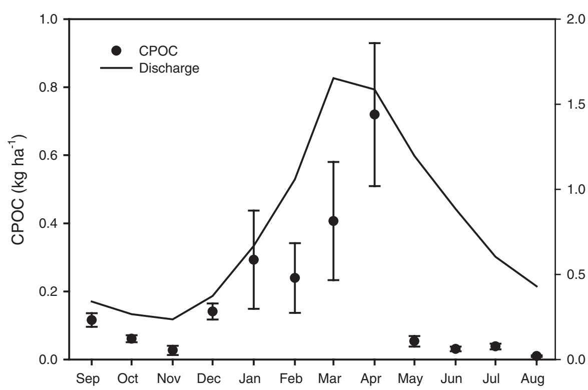

Figure 2. Coarse particulate organic carbon exports in streamwater from four forested headwater catchments near Juruena in the southern Amazon, 2003–2004. Mean monthly stream discharge is plotted as a solid line. CPOC data presented as mean ± 1 SE (N = 4 watersheds).

Table 4. Particle size distribution of coarse particulate organic matter exports from forested headwater streams in the southern Amazon. Values presented are mean ± 1 SE for eight samples in each season. Size fractions determined from 7.9-mm and 2.4-mm sieves, with large fraction > 7.9 mm, 2.4 < medium fraction < 7.9 mm, and smallest fraction < 2.4 mm.

Fraction	Wet season % of total	Dry season % of total
Large	35.6 ± 7.1	85.1 ± 4.0
Medium	25.7 ± 2.3	9.9 ± 3.1
Small	38.7 ± 7.2	5.1 ± 1.1

DISCUSSION

Litterfall dynamics

The litterfall rates determined for Juruena, Mato Grosso are within the range of those reported in other studies conducted within primary forests of the Amazon basin: 8.0 Mg ha^{-1} y^{-1} (Luizão 1989); 8.4 Mg ha^{-1} y^{-1} (Martius *et al.* 2004); 9.2 Mg ha^{-1} y^{-1} (Barbosa & Fearnside 1996); 9.7 Mg ha^{-1} y^{-1} (Smith *et al.* 1998) and 12 Mg ha^{-1} y^{-1} (Rodrigues *et al.* 2000). Due to the variability in methodologies used by different researchers (Proctor 1983), further comparisons of the results of the present study with those in the literature are limited to total litterfall and the leaf fraction of litterfall and their C concentrations.

Litterfall rates in Juruena were more than double in the dry season than in the wet season. This is consistent with studies conducted by Cuevas & Medina (1986), and Barbosa & Fearnside (1996) who also found the highest litterfall rates during the dry season. This feature is likely due to the development of water stress during the dry season, and is typical of semi-deciduous forests with strong seasonality, where peak leaf deposition of litterfall in the dry season represents the vegetative response to seasonality (Arato *et al.* 2003).

A peak in litterfall deposition during the rainy season was also observed (Figure 1, January). This characteristic was also noted by Arato *et al.* (2003) and Araújo *et al.* (2002) in semi-deciduous forests. According to Luizão (1989), there is a positive relationship during the rainy season between rainfall intensity and litterfall rates, whereby intense precipitation coupled with high winds that followed brief dry spells (5 consecutive rain-free days) produced high rates of litterfall.

In the present study as well as in other Amazonian litterfall studies, the leaf fraction was the largest litterfall component. Our results (leaf fraction equivalent to 50% of litterfall) are slightly lower than the leaf component of litterfall reported for Amazonian forests by Barbosa & Fearnside (1996) and by Martius *et al.* (2004), where leaves comprised about 61% and 67% of total litterfall, respectively. However, the leaf-fraction litter flux for the present study (5.9 Mg ha^{-1} y^{-1}) is on par with that found by Martius *et al.* (2004) (5.6 Mg ha^{-1} y^{-1}).

The mean C concentration of total litterfall for the period of study is consistent with the C concentration of litterfall found in the central Amazon (Luizão 1989) and the northern Amazon (Barbosa & Fearnside 1996). The litterfall C flux is higher than that reported for the less strongly seasonal central Amazon (Luizão 1989) (4 Mg C ha^{-1} y^{-1}), but is within the observed range for tropical forests (Clark *et al.* 2001, Malhi *et al.* 2004). The higher C concentration in the miscellaneous and branch fractions compared with the leaf fraction is consistent with other studies (Chan 1982).

Litter movement across the landscape

The higher lateral transport of litter during the dry season compared with the rainy season (Table 2) suggests the importance of other factors including wind (Benfield 1997) in the lateral movement of litter. However, the higher litterfall rates during the dry season indicate that more material is available to transport during that period. Normalizing the lateral transport rate during each season by the seasonal litterfall rate shows the specific lateral transport rate to be 71% higher in the wet season (average of all landscape positions).

Mean monthly throughfall was not found to be significantly related to the lateral movement for any landscape position. In other studies of the lateral movement of litter, Magana (2001) did not find a relationship between precipitation and litter transported by overland flow, while Scarsbrook *et al.* (2001) showed a significant and positive correlation ($R^2 = 0.26$; $P = 0.02$) between total precipitation and lateral entry of litter into streams. These differences are likely due to variation in site characteristics (forest type and topography) and methodologies employed in the studies. Both Magana (2001) and Scarsbrook *et al.* (2001) employed bank-side lateral litter collectors exclusively, while traps were placed in various landscape positions in the present study.

Among landscape positions, the plateau position exhibited reduced lateral movement of litter in both wet and dry seasons compared with the steeper riparian hillslope (Table 2). This suggests that it is the interaction of morphologic and microclimatic factors that more strongly controls the movement of litter into streams, as suggested by McClain & Elsenbeer (2001).

Coarse particulate watershed exports

Coarse particulate watershed exports exhibited strong seasonality, with almost six times greater exports during the wet season than in the dry season (Table 3). This is a natural consequence of the pulsing nature of CPOC exports, which are strongly tied to larger storm events, which was also observed by Wallace *et al.* (1995).

The relationship between precipitation and CPOM export has been observed by a number of researchers (Mulholland 1997, Scarsbrook *et al.* 2001, Wallace *et al.* 1991, 1995). During this study, February was the month with the greatest volume of throughfall, while March was the month with the highest stream water discharge. However, April was the month with the largest exports. Throughfall during April fell on soils that were at their highest moisture status during the study (M. Johnson, unpubl. data). In addition, precipitation intensity was highest during April, with several storms producing 5-min intensities of over 150 mm h^{-1}, which would likely contribute to higher CPOM exports.

Dry-season CPOM exports were dominated by the largest size fraction (Table 4), whereas wet-season exports exhibited a much higher degree of biophysical breakdown of materials, both in-stream and on the terrestrial landscape prior to its export in streamflow. The dominance of the larger size fraction during the dry period is likely due in part to higher litterfall rates during the dry season (including direct litterfall into streams) which could overwhelm the ability of in-stream detritivores to breakdown allochthonous materials prior to their downstream export. Wetted stream perimeter is also higher during the wet season when streamflow is higher, which would contribute to additional biological activity in the stream. Additionally, the lower C concentrations of laterally transported litter during the wet period (Table 3) indicate that the material being washed or blown into the stream is also more highly processed during the wet season.

From litterfall production to stream export

Streamwater export of CPOM represents only about 0.03% of mean annual litterfall production (11.8 Mg ha^{-1} y^{-1}). In addition to being small relative to litterfall, coarse particulate organic carbon exports are a relatively minor component of streamwater exports of organic C from the studied catchments (3.5%). However, the values are in the range reported by Wallace *et al.* (1995) for Appalachian streams, where CPOM represented 1.8–3.8% of watershed exports of organic matter. In another temperate zone study, Shibata *et al.* (2001) report the particulate fraction (0.45 μm–10 mm) of C exports as 4% of total. Currently, no other comparable study exists within tropical environments that can be contrasted to this study. Assuming a steady state of sources and sinks, most of the litterfall C must have been decomposed and emitted as carbon dioxide, incorporated into soil organic matter, or transported in the form of dissolved organic C.

The mean C concentration of CPOM during the period of study (43%) was less than that of gross litterfall (48% C), but comparable to the C concentration of lateral litter-C for the near-stream RH position. The reduction in C concentration relative to litterfall is a result of early stages of litter decomposition in the terrestrial environment and subsequent biophysical processing in first-order streams. That C concentration decreased along a toposequence indicates that the transported litter was more degraded in lower landscape positions compared to higher positions.

Litter C transport was higher for the steeper landscape positions (upper hillslope and riparian hillslope) in both wet and dry seasons compared with the plateau position, but the hypothesis that litter transport would be greater on steeper slopes was only found to be true for the dry season. Contrary to our second hypothesis, litter exported by headwater streams was unrelated to litterfall production at monthly and seasonal scales, but was instead dependent upon stream discharge.

ACKNOWLEDGEMENTS

NASA LBA-ECO grant to project group ND-11, Universidade Federal de Mato Grosso; Cornell University; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior-CAPES. The authors greatly appreciate the collaborations of field site hosts Rohden Indústria Lígnea Ltda. and Apolinário Stuhler, and thank Benedito Silveira de Andrade and Elielton Anterio da Souza for field assistance. The comments provided by three anonymous reviewers were very helpful in improving the paper.

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