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Organic carbon fluxes within and streamwater exports from headwater catchments in the southern Amazon

Mark S. Johnson,[1]* Johannes Lehmann,[1] Evandro Carlos Selva,[2] Mara Abdo,[3] Susan Riha[1] and Eduardo Guimarães Couto[2]

[1] *Department of Crop and Soil Sciences, Cornell University, Ithaca, NY 14853, USA*
[2] *Department of Soil Science, Federal University of Mato Grosso, 78060-900 Cuiabá, MT, Brazil*
[3] *Instituto de Biociências, Universidade Federal de Mato Grosso, 78060-900 Cuiabá, MT, Brazil*

Abstract:

Forms and quantities of organic carbon (C) fluxes at the soil surface, and organic C exports from four small (1–2 ha) headwater catchments were quantified and contrasted in the seasonally dry southern Amazon for 1 year to compare C fluxes within the terrestrial ecosystem with exports to the aquatic ecosystem. At the soil surface, the flux of litterfall C was 43 times greater than the dissolved organic carbon (DOC) flux in throughfall, with the highest rates of C deposition during the dry season. The form and timing of organic C was reversed for watershed exports, where DOC comprised 59% of the annual total organic C export, and exports were greatest during the 4-month rainy season (63% of total annual exports). Fine particulate organic carbon (FPOC) in streamwater was a substantially larger flux than coarse particulate organic carbon (CPOC), representing 37 and 4% of total annual organic C exports, respectively. Particulate organic C exports exhibited substantial seasonal variability, with FPOC and CPOC mobilized primarily in the rainy season and strongly connected to storm events. Storm flow comprised 6% of total streamflow for the year studied, and 10% of streamflow during the rainy season. In the rainy season, over 90% of FPOC exports were transported by storm flow, while only 32% of DOC exports were exported by storm flow during this period. Streamwater DOC concentrations were found to increase linearly with increasing terrestrial litterfall during the dry season ($r^2 = 0{\cdot}92$, $p < 0{\cdot}001$), indicating that in-stream processing of allochthonous litterfall is an important source of DOC during the dry season. Copyright © 2006 John Wiley & Sons, Ltd.

KEY WORDS dissolved organic carbon; DOC; particulate organic carbon; POC; litterfall; throughfall; overland flow; tropical watershed

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INTRODUCTION

Carbon (C) transformations and retention within ecosystems and losses from them is an ongoing area of intense investigation at multiple scales and in a range of disciplines. Stream ecologists recognize terrestrial C as the primary energetic basis of the aquatic food web in headwater catchments (Cummins *et al.*, 1983), while terrestrial C mobilized in streams is also a fundamental feedback to the atmosphere through in-stream mineralization and outgassing (Mayorga *et al.*, 2005; Richey *et al.*, 2002).

Measurement of C fluxes at ecosystem interfaces provides a means of quantifying C forms, flows and transformations, while a comparison between the atmospheric–terrestrial interface and the terrestrial–aquatic interface allows the determination of the net results of processes occurring within the terrestrial ecosystem. Organic C is of particular interest as it provides energetic sources to biological activities and a form for

* Correspondence to: Mark S. Johnson, Department of Crop and Soil Sciences, Cornell University, Ithaca, NY 14853, USA.
E-mail: msj8@cornell.edu

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potential C sequestration, and is first acquired and then transformed, retained or lost from the ecosystem of interest.

Headwater catchments provide a scale of study in which C transformations and flows occurring in the soil can be quantified at a landscape scale. Headwater catchments occupy the bulk of the landscape, comprising 70–80% of the terrestrial environment (Gomi *et al*., 2002). Headwater streams are also a major component of the aquatic system. In the central Amazon, first-order streams were found to account for 65% of total stream length in a mesoscale watershed (McClain and Elsenbeer, 2001). First-order streams provide opportunities for elucidating and quantifying processes occurring in the terrestrial environment (Jones and Mulholland, 1998), whereas soil–stream linkages become less apparent with increasing downstream distances from headwater catchments (Hope *et al*., 2004).

At the terrestrial–atmospheric interface, organic C is delivered from aboveground biomass as litterfall and as dissolved organic carbon (DOC) in throughfall and stemflow. Organic C fluxes at the terrestrial–aquatic interface are composed of DOC in surface and groundwater contributions to streamflow, fine particulate organic carbon (FPOC) transported by water fluxes, and coarse particulate organic carbon (CPOC) delivered as direct litterfall onto streams and transported from the soil litter layer by overland flow and wind (McClain and Elsenbeer, 2001; Wallace *et al*., 1995).

Biotic and abiotic processes occurring at and between these two interfaces result in transformations in the quantity, composition and mobility of organic C. For example, decomposition of the soil litter layer results in the formation of humus, mobilization of DOC and loss from the organic pool as CO_2 via soil respiration. Similarly, the processing of C in the benthic layer of streams alters the form of C available downstream.

We investigated organic C fluxes within the terrestrial environment and exports of organic C from forested headwater catchments over the course of a water year in the southern Amazon. The objectives of this study were to (1) compare the timings and magnitudes of organic carbon fluxes at the forest floor with those exported from the headwater catchments, and (2) determine the magnitude of coarse and FPOC exports from headwater watersheds relative to DOC exports.

METHODS

Site characterization

The study was conducted in four adjacent, small (1–2 ha) headwater catchments in an undisturbed forest near Juruena, Mato Grosso, in the seasonally dry southern Amazon (10°25′S, 58°46′W, 230–250 m asl). The landscape in the region is typical of the gently undulating hills of the Brazilian shield. Each watershed is composed of a nearly flat plateau, hillslope, riparian zone and first-order stream (Figure 1). A spring located at the interface of the hillslope and the riparian zone in each watershed gives rise to a small stream flowing through a narrow (<5 m) riparian zone over a streambed composed of sand silt and clay. Vegetation on the terra-firma is forested, with a number of palm species including *Iriartea exorrhiza* Mart. and *Oenocarpus bataua* Mart. in the mixed forest community in the riparian zone.

Precipitation during the study year totaled 2379 mm and followed a unimodal distribution, with 70% of the annual total falling during the rainy season. Air temperatures in the forest ranged from 16 to 32 °C, and streamwater temperatures ranged from 18 to 27 °C. Stream characteristics are presented in Table I.

Soils in the watersheds are deep and acidic, consisting primarily of Oxisols and Ultisols, with a greater increase in clay content at depths distinguishing the Ultisols from the Oxisols. Soils were collected in 2003 from a 20 × 20 m sample grid in each watershed, resulting in 37–64 sample points per watershed in relation to watershed size. Composite samples were collected from 0–20 cm from five points within 1 m^2, while single samples were collected from 40–60 cm. General soil characteristics are presented in Table II.

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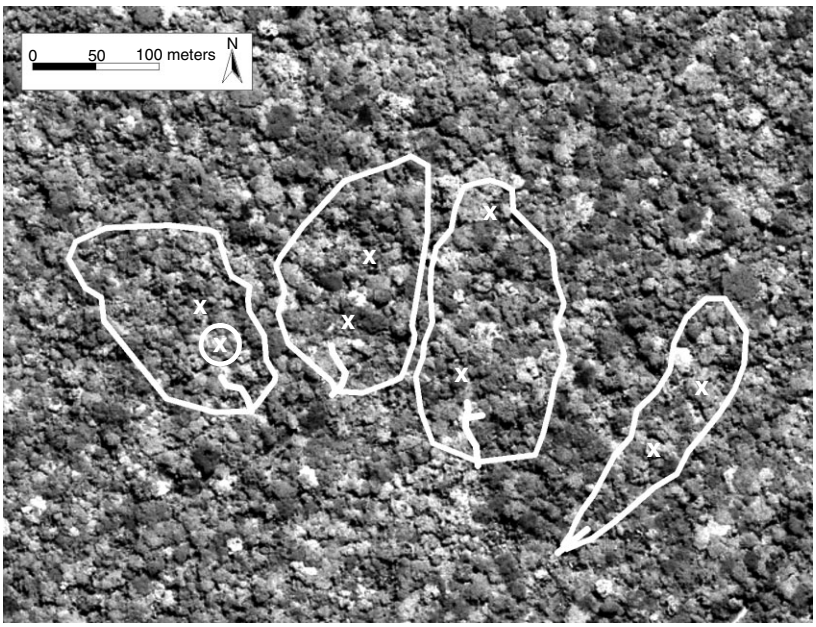

Figure 1. Study location near Juruena, Mato Grosso, Brazil, depicted with watershed delimitation and streams overlain on a 2002 IKONOS panchromatic image of the forested study location, courtesy EOS-Webster. Groundwater well locations are marked by X. The data presented in Figure 2 corresponds to the circled groundwater well

Table I. Average forested headwater stream characteristics for four 1–2 ha watersheds in Juruena, Mato Grosso. Electrical conductivity and pH are volume-weighted means within each watershed averaged across study area, September 2003–September 2004

	Minimum	Maximum	Average[a]
Electrical conductivity (μS cm^{-1})	9	114	35 ± 4
pH	4·62	6·88	$5{\cdot}70 \pm 0{\cdot}16$
Stream length (m)	15	50	$35 \pm 8{\cdot}5$
Discharge			
Average (l s^{-1})	0·5	1·2	$0{\cdot}7 \pm 0{\cdot}2$
Minimum daily (l s^{-1})	0·06	0·20	$0{\cdot}1 \pm 0{\cdot}03$
Maximum instantaneous (l s^{-1})	15	48	$31{\cdot}5 \pm 7{\cdot}6$

[a] Average values for means of watersheds ±1 SE ($n = 4$ watersheds).

Instrumentation and sampling

At each watershed outlet, a 90° V-notch weir was constructed and was instrumented with a recording capacitance rod with thermistors measuring water and air temperatures (TruTrack, Christchurch New Zealand). A staff gauge was also installed to provide an additional, physical measurement of the water level. Recorders were set to take readings every minute and to log data at 5-min intervals averaged from the 1-min readings. Groundwater wells were installed at upper and mid-slope positions in each watershed (Figure 1). The depth to the water table was measured manually each week (biweekly during dry season). These 8-m wells were constructed of 5-cm diameter PVC pipes slotted over the lower 1·5 m.

A coarse organic matter trap was fixed on the downstream side of the weirs, consisting of a box frame (1 m^3) lined with 2-mm mesh on its top, bottom and all sides except on the weir side (i.e. entrance to the

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Table II. Representative soil characteristics of four study watersheds (1–2 ha), Juruena, Mato Grosso. Thirty-seven to 64 individual soil samples were collected in each watershed in 2003. Values are averages of means of watersheds ±1 SE (i.e. $n = 4$). Data are summarized from Novães Filho (2005)

	0–20 (cm)	40–60 (cm)
pH[a]	4·07 ± 0·01	4·31 ± 0·04
Organic C (mg g^{-1})	9·8 ± 0·2	5·3 ± 0·2
Clay (%)	31·7 ± 3·6	42·6 ± 1·5
Silt (%)	5·3 ± 0·9	8·5 ± 1·7
Sand (%)	63·1 ± 4·4	48·9 ± 3·0
Cation exchange capacity (CEC) ($cmol_c$ dm^{-3})	4·40 ± 0·18	7·72 ± 0·43

[a] Soil pH measured in 0·01 M $CaCl_2$ solution, 1 : 2·5 w/v.

trap). The bottom of the box was attached 15 cm below the weir notch so as to not impede free discharge over the weir, and the exit side of the box was fitted with a panel that could be raised to facilitate collection of material retained in the trap.

Springs were fitted with an open PVC pipe inserted into the hillslope at the focal point of groundwater emergence. A hose was connected to the pipe to facilitate collection and to ensure that the emergent groundwater of the spring was sampled prior to any contact with the riparian zone or streambed. In all installations where plastics were used, new materials were conditioned prior to installation for 72 h by submerging them in a flowing stream adjacent to the study catchments (DOC < 1 mg l^{-1}).

Two passive stormflow collectors were attached to each weir and shielded from direct light to prevent UV degradation of DOC via photolysis. The collectors consisted of an entrance tube fixed to the discharge side of the crest of the weir. These were designed such that as rainfall events raised the water level at the weir, the lower stormflow collector filled; if the water level rose sufficiently, a second stormflow collector filled. The entrance tubes were placed on the weirs at heights corresponding to approximately 10 and 20 times minimum discharge. The collection bottles were fitted with vertically oriented ventilation tubes allowing air to be displaced as the bottles filled. The free end of the flexible ventilation tube was looped over and sited to avoid contact with precipitation and splash from rainfall. The narrow (5 mm) internal diameter of the ventilation tubes ensured that discrete samples were collected. For example, the stormflow collector bottle filled rapidly once the water level rose to the level of the collection tube. A subsequent 10 cm rise in water level at the weir above the level of the stormflow collector fill tube also raised the water level in the ventilation tube by 10 cm, but this rise displaced only 0·6% of the 300-ml storage volume of the stormflow collection bottle.

In each watershed, a below-canopy recording rain gauge was paired with a separate throughfall collector for a total of four pairs of throughfall collectors and recorders in the study area. The collector consisted of a 200 cm^2 funnel lined with glass wool placed over a throughfall collector bottle and attached to a stake 1 m above the ground. The rain gauge was installed in parallel with each throughfall collector, and comprised a tipping-spoon rain gage with a 200 cm^2 orifice (Pronamic, Silkeborg Denmark) wired to an event data logger (Onset Computer Corp., Pocasset, USA). Throughfall volumes and DOC concentrations were reported as an average of the four gauges and collectors, respectively.

Overland flow collectors were installed at mid-slope positions where overland flowpaths were apparent, with one collector installed per watershed. These consisted of a 3-m length of PVC tube (75-mm diameter), the upslope end of which was in contact with the ground and the opening was lined with 2-mm mesh to prevent the accumulation of litterfall inside the tube. Stakes were used to anchor and support the downslope end of the tube at an angle slightly less than the soil slope, allowing storage of overland flow in the tube and space for sample collection without disturbing the collector. A faucet was installed in an end-cap attached

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to the downslope end of the tube, facilitating collection of overland flow. For collection of overland flow samples, the faucet was opened and stored water was allowed to run until the slug of accumulated silt was flushed (5 s). The collection bottle was then filled, and the faucet left opened until the overland flow collector ran dry. Accumulated litter at the tube entrance was removed weekly.

A recording overland flow detector was paired with each overland flow collector. These were constructed in the same fashion as the overland flow collectors, and were installed parallel to the overland flow collectors. However, instead of having a faucet at the downslope end, the overland flow detectors were perforated with a drain hole, and a data-logged tipping bucket was placed under the hole. Overland flow DOC concentrations are presented as the average of the four collectors, while the timings of overland flow and throughfall were compiled for 5-min time steps throughout the course of the study.

Litterfall was collected in four 1-m^2 litter traps per watershed installed at randomized locations. Litterfall traps consisted of a mesh base (2 mm openings) attached to a PVC frame and mounted on stilts 1 m above the ground surface. A 30-cm wind shield of woven polyethylene feed sacks was placed around the litter traps to prevent accumulated litter from blowing out of the trap prior to its biweekly collection.

Water samples were collected weekly during the rainy season and biweekly during the dry season. Additional samples were collected in conjunction with storms occurring during the dry season. Material retained in the weir traps was collected at the time of water sampling. Determinations of pH and electrical conductivity were made in the field for water flowing freely over the weir using a combination meter (Hanna Instruments model HI98129, Woonsocket, USA). Baseflow grab samples were collected from streams and stormflow samples were collected if present, as were throughfall and overland flow samples. Water samples were collected from springs at the same intervals as for streamwater, but began two months later than streamwater collections, as groundwater recharge was necessary to ensure that the springs were flowing at rates conducive to measurement and collection.

Analytical methods

Water samples were filtered within 24 h of collection (Whatman GF/F glass fiber filters, 0·7 μm, Middlesex, UK), preserved with $HgCl_2$ to adjust sample concentration to 30 μM Hg, and stored in pre-muffled glass vials with Teflon-lined tops at 3 °C until analysis (McClain *et al*., 1997). DOC was determined chromatographically after combustion in a total organic carbon (TOC) analyser (Multi N/C 3000, Analytik Jena, Jena Germany) at the Federal University of Mato Grosso (UFMT) using the non-purgable organic carbon (NPOC) method. Filters were stored at 3 °C in aluminium foils, then oven-dried to constant mass at 60 °C prior to combustion in a high-temperature furnace (Eltra HTF-540, Neuss, Germany). CO_2 resulting from the combustion of organic matter retained on the filters passes to the in-line TOC analyser, permitting the determination of the amount of FPOC retained on the filter for the volume of water filtered (300 ml), which we report here as concentration (mg l^{-1}).

Materials removed from the weir traps were air dried, and shipped to the UFMT laboratory where they were oven-dried to constant mass and ground. A representative sub-sample was combusted in the high-temperature furnace and the C content used to compute CPOC in the sample (Tiessen and Moir, 1993). Litterfall was processed in the same manner as materials retained on the weir trap.

Discharge was computed from the water level measurements at the weir. The percentage of daily streamflow attributable to storm flow was determined from the 5-min hydrograph. To determine DOC and FPOC fluxes during each collection interval, the average DOC and FPOC concentrations in the grab samples were applied to the baseflow fraction of discharge, while average stormflow concentrations were applied to the stormflow fraction of discharge. As such, average stormflow concentration values were determined for each collection throughout the year from all stormflow collectors that contained samples (up to eight collectors per week). CPOC fluxes were determined from the amount of CPOC retained on the weir traps during the collection interval.

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RESULTS AND DISCUSSION

Above-ground carbon fluxes to soil surface

Fluxes of both litterfall C and throughfall DOC exhibited strong seasonality linked to seasonal patterns in throughfall volumes (Figure 2A and B). During the May–September dry season, litter production increased as soil moisture became limiting and leaf senescence increased. The litterfall for the period of study, 5·89 Mg C ha^{-1} yr^{-1}, is near the upper end of litterfall production for tropical forests globally (Clark *et al*., 2001; Malhi *et al*., 2004), but is similar to litterfall rates reported for an undisturbed central Amazonian forest (Rice *et al*., 2004).

The flux-weighted average throughfall DOC concentration for the study year was 6·2 mg l^{-1}, with a throughfall DOC flux of 14·9 g m^{-2} yr^{-1}. These values are in close proximity to those of other studies for forested areas in the Neotropics (Table III).

Throughfall DOC fluxes to the soil surface were driven by two factors that are inversely related at a seasonal timescale: throughfall volumes and DOC concentrations. The highest concentrations of DOC in throughfall were found following long dry periods, reaching a maximum of $96{\cdot}1 \pm 10{\cdot}6$ mg DOC l^{-1} (average ± 1 SE, $n = 4$ watersheds) following 41 days without rain. At the other extreme, the minimum throughfall DOC concentration detected during the period of study was $2{\cdot}41 \pm 0{\cdot}28$ mg l^{-1} (average ± 1 SE, $n = 4$) during the onset of almost daily rains during the rainy season and following more than 400 mm of throughfall that had passed through the forest canopy during the dry-to-wet season transition (September–December).

Two distinct phases of throughfall DOC fluxes were present over the course of the study: that of numerous and significant rainfall events during the rainy season transferring large volumes of relatively dilute throughfall DOC concentrations from the forest canopy to forest floor, and that of storms occurring during the dry season and dry-to-wet season with high DOC concentrations in throughfall. Neither phase dominated the total annual flux. During the 4-month rainy season, the total throughfall DOC flux was 6·8 g m^{-2}, compared with 8·1 g DOC m^{-2} during the dry and dry-to-wet seasons combined. Seasonal variability of throughfall DOC concentrations has been observed in both tropical and temperate regions (Filoso *et al*., 1999; Kindlmann and Stadler, 2004).

Overland flow DOC concentrations exhibited seasonality that tracked the seasonal trends of both litterfall flux and throughfall DOC concentrations (Figure 2B and C). In general, DOC concentrations in overland flow were higher than those of throughfall DOC, indicating further DOC production as throughfall interacts with the litter layer of the forest floor (Hinton *et al*., 1998). The mean (non-flux weighted) DOC concentration of overland flow during the study year was 19·7 mg l^{-1}. The large temporal variability observed (Figure 2C) is typical of seasonal trends in overland flow DOC. Hinton *et al*. (1998), working in forests of eastern Canada, found that DOC concentrations in overland flow ranged up to 120 mg l^{-1} while annual average concentration was about 9 mg l^{-1}.

Overland flow is not typically a component of DOC studies at the watershed scale, since it is generally not a significant hydrologic flowpath of forested catchments (Qualls *et al*., 2002). Overland flow is also a

Table III. Annual average throughfall DOC concentrations and fluxes for forested areas in the Neotropics

Location	Throughfall DOC		Study
	Concentration (mg l^{-1})[a]	Flux (kg ha^{-1} yr^{-1})	
Northwestern Amazônia	6·70	190	Tobón *et al*. (2004)
Northern Amazônia	8·1	83·1	Markewitz *et al*. (2004)
Central Amazônia	9·72	159	Filoso *et al*. (1999)
Luquillo Mountains, Puerto Rico	6·16	128	McDowell (1998)
Southern Amazônia	6·19	149	Present study

[a] Flux-weighted averages.

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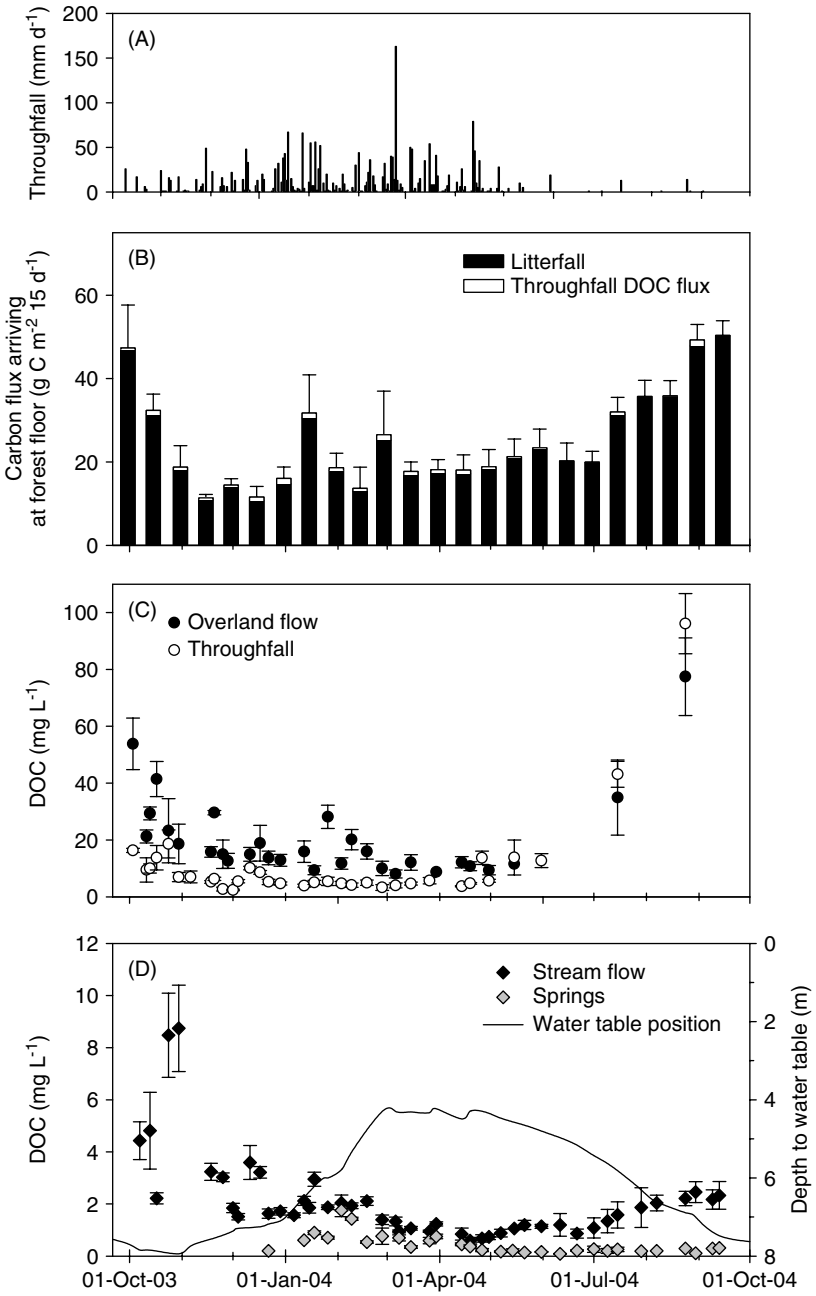

Figure 2. Throughfall measurements over study period in mm day^{-1} (A), above-ground C fluxes of litterfall C and throughfall DOC to the soil surface (B), aboveground terrestrial DOC concentrations (C), and DOC concentrations in grab samples from streamflow and springs together with position of water table at mid-slope (D). Data is mean ± 1 SE for $n = 4$ watersheds, except for water table position, which is presented for the groundwater well circled in Figure 1

spatially and temporally diffuse flowpath, and is difficult to quantify on a watershed basis owing to associated processes including reinfiltration and exfiltration of return flow (Walter *et al*., 2005) and emergence of pipe flow (Elsenbeer and Vertessy, 2000). It is, nonetheless, a significant hydrologic feature of the headwater

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catchments of the study area. Overland flow was detected in 5·8% of the more than 100 000 five-minute intervals logged during the study year, as compared to throughfall, which was detected during 5·4% of the time steps. This indicates that the presence of overland flow was observed during 508 h over the course of the study year, compared with 473 h of throughfall during the study year. Generally, overland flow was generated rapidly with the onset of throughfall, and persisted for some time after the end of the storm. The average overland flow DOC concentration during the period of study (19·7 mg l^{-1}) is in the range of published values of DOC concentrations of overland flow for forested watersheds: 35·0 mg l^{-1} for NW Ontario (Allan *et al*., 1993) and 14·1 mg l^{-1} for South Australia (Chittleborough *et al*., 1992).

The flux of litterfall C was found to be 43 times greater than throughfall DOC on an annual basis. A comparison of these fluxes at 2-week intervals found that the ratio between litterfall and throughfall C fluxes (LF C : TF DOC) ranged from 11 to 1106, representing a rainy period with relatively low litter production for the lower value, and a period of high litterfall and low rainfall for the higher value. Excluding the dry-season period from the analysis, an average ratio (LF C : TF DOC) of 22 was found.

Several additional components of non-gaseous C fluxes at the soil surface were not included in the analysis of solid *versus* dissolved C fluxes. Stemflow, which contributes only 1–2% of total precipitation arriving at the forest floor in Amazonian forests (Lloyd and Marques, 1988; Tobón Marin, 2000), was not analysed in the present study. While stemflow DOC concentration is typically several times greater than throughfall (Liu and Sheu, 2003), it represents a small total flux of DOC that follows the same temporal dynamics as the larger throughfall DOC flux. The flux of coarse woody debris (CWD, >2-cm diameter) from the canopy was not considered in the present study of seasonal C dynamics because of the slower turnover time of CWD. There is an order of magnitude difference in decomposition rates between litter (~1 year reported for tropical forests in Clark *et al*. (2001)) and CWD (9 years as reported in Keller *et al*. (2004) for the Amazon). In addition, the contribution of FPOC, which would have passed through the 2-mm mesh of the litterfall traps and was excluded from the throughfall collectors by the glass wool filter, was not included in the analysis.

The exclusion of FPOC flux to the soil surface, coupled with potential decompositional losses of throughfall DOC in the field prior to collection, suggests that both terms of the LF C : TF DOC ratios were underestimated. In a study of decomposition of dissolved organic matter (DOM) in samples of throughfall, Qualls and Haines (1992) found that 94, 89, and 83% of original throughfall DOC remained after incubations of 2, 4, and 7 days, respectively. Inspection of the rainfall record against the dates of the weekly sample collection interval found that throughfall samples were stored in the sample collection containers in the field for an average of 4 days prior to collection during the rainy season, suggesting a loss of about 10% of DOC prior to sample preservation. Samples were typically collected within a day of rainfall during the dry season. The percentage of litterfall contained in the <2 mm fraction is uncertain, since 2 mm is the typical mesh size used in litterfall studies (Clark *et al*., 2001). If, for example, the exclusion of very fine litterfall (FPOC) due to the 2-mm mesh size caused a 5% underestimate in litterfall C, and throughfall DOC was underestimated by 10%, the annual LF C : TF DOC ratio would have been 41 rather than the ratio of 43 reported. Including the slower turnover pool of CWD in the analysis (using literature values of 2·5 Mg C yr^{-1}, assuming *ca* 50% carbon content of CWD (Clark *et al*., 2002) and deposition rates of ~5 Mg CWD yr^{-1} (Clark *et al*., 2002; Keller *et al*., 2004)) would have resulted in a ratio of solid OC to dissolved OC at the forest floor of 58.

Organic carbon exports from watersheds

DOC was found to comprise the largest component of organic C exports, representing 59·5% of the annual total. FPOC (37·0% of total) was also found to be a substantial flux, while CPOC (3·5% of total) was a relatively minor component of total headwater exports of organic C. Few studies have compared dissolved, fine and coarse particulate organic matter for headwater catchments, with the notable exception of that by Wallace *et al*. (1995) at the Coweeta LTER experimental watersheds in North Carolina. In their work, Wallace *et al*. (1995) also found that the coarse C fraction was a minor (1·8–3·8%) component of total organic C exports.

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Watershed exports totaled 31·5 kg ha^{-1} yr^{-1} for DOC and 17·6 kg ha^{-1} yr^{-1} for POC (FPOC plus CPOC). These values are in the range of DOC and POC exports for non-montane forested headwater (1st order) catchments reported in the literature (Table IV).

In the present study, the ratio between solid and dissolved forms of organic C exports from the headwater catchments stands in contrast to the fluxes arriving at the forest floor (Figure 3), demonstrating a transition from C inputs at the soil surface dominated by the solid form to watershed organic C exports dominated by the dissolved form. *In situ* decomposition of litter on soils was clearly an important factor, as the soil litter layer in the study watersheds was observed to be largely exhausted by the end of the rainy season, even for areas of the watersheds with little topographic relief.

Table IV. Exports of DOC and POC from non-montane, forested headwater catchments

Catchment, location	DOC	POC	DOC : POC	Study
	(kg ha^{-1} yr^{-1})			
Coweeta C53, North Carolina	11·6	27·9	0·41	Wallace *et al*. (1995)
West Fork Walker Branch, Tennessee[a]	8·3	18·0	0·46	Mulholland (1997)
Satellite Branch (WS55), North Carolina[a]	3·7	7·4	0·50	Wallace *et al*. (1997)
Coweeta C55, North Carolina	9·9	15·5	0·64	Wallace *et al*. (1995)
Coweeta C54, North Carolina	10·3	11·4	0·90	Wallace *et al*. (1995)
Breitenbach, Germany[a]	2·9	1·9	1·51	Marxsen *et al*. (1997)
Augusta Creek, Michigan[a]	45·3	29·6	1·53	Webster and Meyer (1997)
Juruena headwater catchments	31·5	17·6	1·79	Present study
Quebrada Toronja, Puerto Rico[a]	33·0	6·5	5·1	McDowell and Asbury (1994)

[a] Dissolved organic carbon (DOC) and particulate organic carbon (POC) computed from dissolved organic matter (DOM) and particulate organic matter (POM) assuming OC = 0·5 OM.

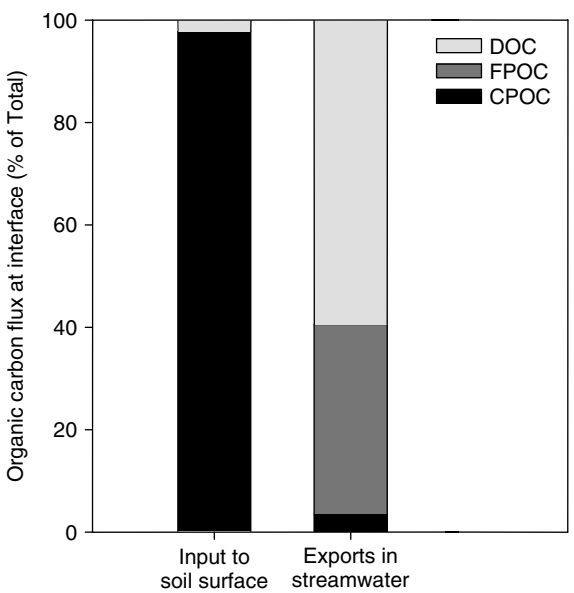

Figure 3. Distribution of organic C forms input to the soil surface in litterfall and throughfall DOC and exports in streamwater. FPOC fluxes at the soil surface were not determined. Data are averages from four headwater watersheds (1–2 ha) in Juruena, Mato Grosso, Brazil. Samples were collected from September 2003 to September 2004

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Significant ($p < 0{\cdot}05$) and positive correlations were found between stream discharge and exports of all organic C size fractions (Table V). Among C exports, DOC and FPOC were found to be significantly associated. While DOC (and to a lesser extent FPOC) was constantly mobilized from headwater catchments, CPOC transport was more episodic in nature, as it was washed downstream from terrestrial, riparian and stream channel locations primarily by storm pulses. The DOC flux of overland flow to the stream was not measured, but a general trend in seasonality of overland flow DOC concentrations is apparent from the samples (Figure 2C). The leaching of fresh litter inputs may explain some of the seasonality in stream DOC concentrations of forested catchments (Hongve, 1999).

During periods of low discharge, whole leaves and larger plant components (i.e. twigs and seeds) dominated the material collected from CPOC traps with 85% represented by CPOC > 8 mm, whereas the CPOC traps following storm events were found to have retained predominantly detrital material, with 64% of CPOC < 8 mm during rainy months (Selva, 2005). The latter illustrates the results of physical abrasion and biological processing already occurring in the first meters of stream passage. This indicates that the simultaneous breakdown (physical and biological) and transport of CPOC, referred to as spiraling (Webster and Patten, 1979), is tied to storm events in the headwater streams studied.

A number of seasons were apparent in the course of a year, each with distinctive characteristics in C fluxes and linkages across the terrestrial–aquatic interface (Figures 3 and 4). In the following sections we will consider the following seasons and characteristics of their respective C fluxes: (1) Dry-to-wet season transition (October–December), (2) Rainy season (January–April) and (3) Dry season (May–September). In particular, the role of storm events in exporting DOC and FPOC fluxes was seen to vary seasonally (Table VI). While the storm flow volume as a percentage of discharge was the highest during the rainy season, the ratio of stormflow DOC concentrations to baseflow DOC concentrations (SF_{DOC}/BF_{DOC}) was lowest. SF_{DOC}/BF_{DOC} was 6·5 during the dry-to-wet season, 4·3 during the rainy season and 5·3 during the dry season.

Dry-to-wet season carbon dynamics at the terrestrial–aquatic interface (October–December)

DOC in overland flow gives an indication of the DOC content in the soil litter layer available to infiltration and run-off. DOC concentrations in overland flow exhibited a strong seasonal pattern tightly coupled with above-ground fluxes to the soil surface (Figure 2C and B, respectively). DOC concentrations in throughfall and overland flow were the highest during this period, generated by sporadic rainfall, and concentrations decreased as rainfall became more frequent (Figure 2C). This seasonal trend was also present in streamwater

Table V. Correlations between various C fluxes in four forested headwater catchments, Juruena, Mato Grosso, during twenty-four 15-day periods for September 2003–September 2004. Cell contents are the p values. Headings are: H_2O, streamflow discharge; DOC, streamflow dissolved organic carbon concentration; FPOC, streamflow fine particulate organic carbon concentration; CPOC, streamflow coarse particulate organic carbon concentration; LF C, litterfall carbon flux at soil surface; and TF DOC, throughfall DOC flux at soil surface

	H_2O	DOC	FPOC	CPOC	LF C
DOC	0·596	—	—	—	—
	0·003	—	—	—	—
FPOC	0·515	0·918	—	—	—
	0·012	0·000	—	—	—
CPOC	0·528	0·262	0·361	—	—
	0·010	0·227	0·091	—	—
LF C	0·273	0·261	0·077	0·175	—
	0·208	0·228	0·726	0·425	—
TF DOC	−0·015	0·378	0·385	0·149	−0·084
	0·945	0·075	0·070	0·499	0·702

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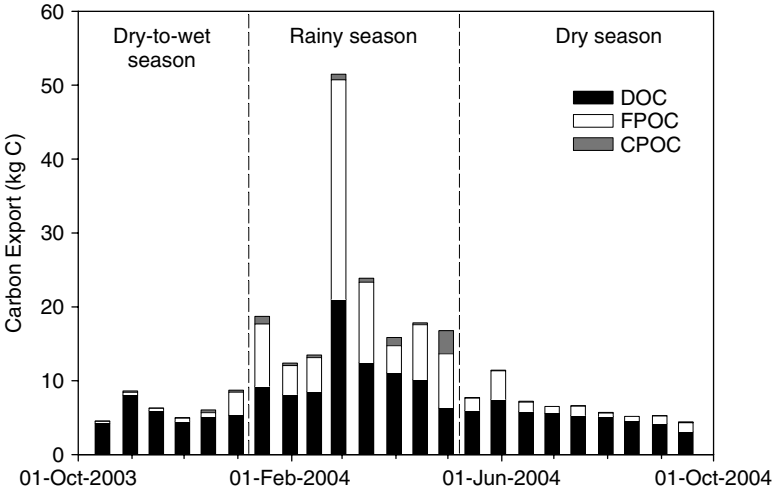

Figure 4. Watershed DOC, FPOC and CPOC exports summed for the four headwater catchments during 15-day intervals indicating distinct seasonal differences between the dry-to-wet season transition (October–December), rainy season (January–April), and dry season (May–September). During the study, $n = 306$ for DOC, $n = 269$ for FPOC and $n = 135$ for CPOC

Table VI. Storm flow as a percentage of total export fluxes, forested headwater catchments, Juruena, Mato Grosso, September 2003–September 2004

Period	Stormflow as percentage of total discharge (%)	Stormflow DOC flux as percentage of total export (n_{bf}, n_{sf})[a]	Stormflow FPOC flux as percentage of total export (n_{bf}, n_{sf})
Season			
Dry to wet	3·2	9·0% (48, 24)	44·2% (22, 21)
Rainy	9·7	32·0% (71, 93)	91·1% (66, 93)
Dry	0·3	1·3% (58, 12)	18·2% (56, 11)
Annual	5·9	19·4% (177, 129)	80·4% (144, 125)

[a] n_{bf}–number of baseflow samples during the period; n_{sf}–number of storm flow samples during the period.

DOC concentrations, suggesting a strong connection between the upper soil profile and stream exports during this period.

Interestingly, deep-soil moisture was depleted by transpiration and deep drainage more rapidly than it was recharged during the first two months of sporadic rains. This was illustrated by decreasing water table depths and the corresponding streamflows, which reached their lowest levels in mid-November, two months after the first rain event of the season (Figures 2D and 5 respectively). Water-table depth in mid-November was greater than 8 m below the surface in upper landscape positions (data not presented; groundwater well installation was limited to 8 m), which could still maintain some transpiration for deeply rooted plants (Nepstad *et al.*, 1994).

Coupling between terrestrial and aquatic ecosystems during the dry-to-wet season can be considered as punctuated, and was dominated by aboveground and near-surface terrestrial processes. Total watershed DOC exports decreased in concert with decreasing DOC concentrations in aboveground DOC flows, even as stream discharge began to increase in mid-November when percolation from rainfall reached deep soil layers and the water table began to rise (Figure 5). Total C exports during this period were predominantly DOC (Figure 4), and over 90% of DOC exports during this period were transported by baseflow.

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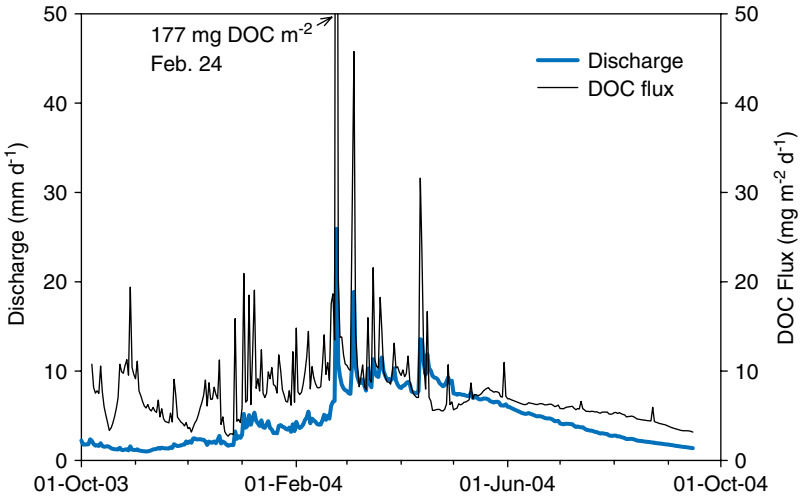

Figure 5. Total watershed discharge and DOC exports. DOC flux decreases relative to discharge during dry-to-wet transition (October–December). During the rainy season (January–April), the discharge increases with DOC constant at seasonal scale. Discharge and DOC flux maxima resulted from a 170-mm rainfall event on 24 February 2004

Rainy season carbon dynamics (January–April)

DOC export from headwater catchments was high and relatively constant at baseflow throughout the course of the rainy season, even as streamflow increased substantially (Figure 5). The water table rose tremendously during the rainy season, reaching to within 4 m of the soil surface in the mid-slope piezometers in the watersheds (Figure 2D).

During the rainy season, the coupling of C fluxes between the terrestrial and aquatic ecosystems shifted to being characterized by more in-soil processes as the volume of water percolating through soils increased and the water table rose. As above-ground biomass and the soil litter layer were subjected to continued canopy exchange and leaching, above-ground DOC concentrations in throughfall and overland flow decreased and became less variable compared to these concentrations during the dry-to-wet season transition (Figure 2C).

Daily fluctuations in DOC exports related to storm events were observed against a background of relatively constant watershed DOC export during the rainy season, although the period was characterized by increasing streamflow that was increasingly more dilute in DOC (Figures 5 and 2D). DOC concentrations in springs averaged 48% of baseflow DOC concentrations of streams during the rainy season.

Stormflow was found to be less than 10% of the total discharge during the rainy season, but was responsible for a third of total DOC watershed exports and over 90% of FPOC exported over this period (Table VI). FPOC in stormflow samples was more than 150 times higher than FPOC in baseflow samples, whereas stormflow DOC was 4 times higher than baseflow DOC during these months. Over 79% of total CPOC exports occurred during the rainy season, with the remainder being exported during the transition season (15%) and dry season (6%).

An additional feature of this period was observed in the DOC concentration of springs, which began to increase shortly after the water table began to rise, peaked in the middle of the rainy season and then decreased again, reaching a minimum concentration when the water table was nearest the soil surface (Figure 2D). This may have resulted from increasing macropore flow as soil moisture increases, giving rise to a hydrologic flushing of DOC from the upper soil profile to springs, which can be considered analogous to the snowmelt-related hydrologic flushing of DOC observed in temperate areas (Boyer *et al.*, 1997).

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Dry-season carbon dynamics (May–September)

Since all streamflow in headwater streams originates as groundwater during baseflow, and no aquatic macrophytes were found in headwater streams of the catchments studied, DOC exports in streamwater were constrained to two sources during the dry season: (1) groundwater DOC and (2) in-stream generation of DOC by decomposition of litterfall in the benthic litter layer of the stream. During the dry season, groundwater DOC concentrations of springs were found to be uniformly low ($0{\cdot}19 \pm 0{\cdot}01$, mean $\pm$ 1 SE), while DOC concentrations in streamwater increased during this period (Figure 2D). Dry season DOC concentration in springs averaged only 14% of DOC concentrations in streamwater at the watershed outlet, indicating that in-stream processes were responsible for the bulk of dry-season DOC exports. Another characteristic of the dry season was increased litterfall, which continuously supplied streams with fresh C inputs. Further evidence of in-stream processing of litterfall as a source of stream water DOC is shown by the positive correlation between increasing concentrations of DOC and FPOC in streamwater during the dry season ($r = 0{\cdot}68$, $p = 0{\cdot}003$, $n = 15$).

Stream water DOC concentrations were found to increase linearly in relation to terrestrial litterfall rates (Figure 6; $r^2 = 0{\cdot}92$, $p < 0{\cdot}001$, $n = 9$ 15-day dry-season time steps). While direct litterfall into streams was not measured, the headwater streams and their adjacent riparian zones are narrow (<5 m) and lined with mature, full-stature trees. Any decreased direct litterfall into streams due to the lack of trees in the stream channel itself would likely be offset by lateral movement of leaves into streams. Lateral movement of leaves, which may be transported by water or blown in by wind (Benfield, 1997), was found to contribute 22 to 27% of leaf input to temperate headwater streams (Wallace *et al*., 1995), and has been estimated as 20% of direct terrestrial litter inputs to Amazonian headwater streams (McClain and Richey, 1996). Lateral movement of leaves in surface leaf detectors was observed in the study catchments (Selva, 2005).

In-stream generation of DOC in headwater streams is driven by processing of allochthonous terrestrial leaf detritus, which is commonly modeled as first-order decay (Webster and Benfield, 1986). The organic C stock in the benthic layer was continuously and substantially replenished by terrestrial litterfall during the dry season, which was broken down rapidly by physical and biological processes. This is especially rapid in the tropics where the average decomposition rate k is $0{\cdot}06$ day^{-1} (Dobson *et al*., 2003; Parnrong *et al*., 2002).

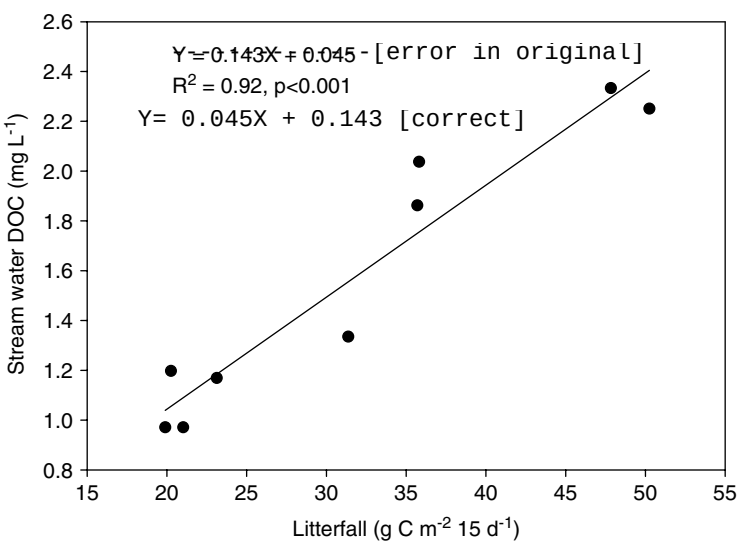

Figure 6. Terrestrial litterfall plotted against 15-day average DOC concentrations in streamwater. Data are averages from four ~1 ha headwater catchments streams in Juruena, Mato Grosso, Brazil. Samples were collected from September 2003 to September 2004

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There was a stronger relationship between the streamwater DOC concentrations and the terrestrial litterfall rate during the dry season than that between DOC concentrations and stream discharge for the same period ($r^2 = 0{\cdot}92$ *vs* $r^2 = 0{\cdot}76$). This indicates that benthic decomposition of litterfall was likely to be the primary source of DOC during the dry season for the headwater catchments studied, in comparison to the spring DOC concentration, which did not vary significantly during this period.

CONCLUSIONS

The form of carbon inputs to the soil surface was found to differ substantially from the form of C in streamwater exports. At the soil surface, litterfall C inputs were found to dominate the total C flux, while DOC was the largest organic C flux exported in the streams from the headwater catchments. The seasonality exhibited by C fluxes at the atmospheric–terrestrial interface was also reversed from those at the terrestrial–aquatic interface. At the soil surface, C fluxes were greatest during the dry season, while the peak for organic C stream exports from the headwater catchments was during the rainy season.

DOC export in streams of the headwater catchments was more closely correlated to litterfall mass than to streamwater flow during the dry season when decomposition of allochthonous litterfall was likely the primary factor for in-stream generation of DOC. On annual and seasonal timescales, exports of CPOC and FPOC from watersheds were low, although input to the soil surface was high. At shorter temporal scales, watershed exports of FPOC and CPOC transported by stormflow were important.

The organic carbon transported by headwater streams to larger streams and rivers has undergone both terrestrial and aquatic processing within the headwater catchments. Significant in-stream processing of terrestrially derived C within 50 m of stream source was found for the low-gradient headwater streams studied, with FPOC and CPOC largely spiraled downstream by stormflow, whereas DOC was more constantly mobilized from the headwater catchments.

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