

Composition and dynamics of allochthonous organic matter inputs and benthic stock in a Brazilian stream

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Abstract. Riparian vegetation provides the nutrient and energy input that maintains the metabolism and biodiversity in tropical headwater streams. In the present study, it was hypothesised that ~30% of riparian plant species contribute over 70% of coarse particulate organic matter and, because tropical plants are perennial and semi-deciduous, it was expected that leaf fall would occur year round. The aims of the present study were to evaluate the composition and structure of the plant riparian zone and the input and associated benthic stock of organic matter. The riparian vegetation was composed of 99 taxa. The most abundant plant species were *Tapirira obtusa*, *Sclerolobium rugosum*, *Croton urucurana*, *Byrsonima* sp. and *Inga* sp. The input and benthic stock showed a seasonal pattern, with higher values recorded at the end of the dry season and at the beginning of tropical storms. The biomass contributed monthly by the vegetation ranged from $28 \pm 6 \text{ g m}^{-2}$ to $38 \pm 11 \text{ g m}^{-2}$, and the mean monthly benthic standing stock was $138 \pm 57 \text{ g m}^{-2}$. The results illustrate the importance of riparian vegetation as an energy source to tropical streams and how individual plant species contribute to organic matter inputs in these ecosystems.

Additional keywords: biodiversity, Cerrado, productivity, rainforest, riparian zone.

Introduction

Autochthonous primary production is often limited in heavily forested catchments because of a well developed canopy cover that reduces light penetration (Wallace *et al.* 1997). As a consequence, allochthonous organic matter is the main energy source for streams in forested catchments (Cummins *et al.* 1973). Riparian vegetation constitutes the transition zone between aquatic and terrestrial ecosystems and is therefore an important functional element of the river landscape (Francis 2006; Richardson *et al.* 2007). The type of marginal vegetation in the riparian zone is determined by climate, hydrological regime and geomorphological origin (Cooper *et al.* 2003). In addition, it plays an important role in the hydrogeomorphological functioning of the ecosystem, influencing the shape and pattern of the river channel (Francis 2006). The structure of the riparian zone is affected by fluvial processes (e.g. flood pulse and soil deposits), and the riparian zone usually has a different species composition than the adjacent terrestrial communities (Prach *et al.* 1996; Naiman and Décamps 1997).

Changes in riparian vegetation can modify the quantity and quality of the organic matter that enters a stream, and can affect the functional processes occurring in a river (Cummins *et al.* 1989; Graça 2001). Preservation of the riparian zone is important for the maintenance of the structure and functioning of lotic ecosystems, especially headwater streams (Lima and Zakia 2000; Gonçalves *et al.* 2006a). Organic matter enters the stream channel either directly (e.g. falling leaves) or through lateral movements during the wet and flood seasons, with the addition of particulate organic matter (POM) (Webster and Meyer 1997). Lateral litter transport depends on the slope of the bank, and on the type, distribution and height of the local riparian plant species, among other factors (Wantzen *et al.* 2008). The spatial and temporal distribution of the quality and quantity of allochthonous organic matter depends on the type of riparian vegetation (Webster and Meyer 1997; Reid *et al.* 2008). Organic matter may be more abundant during a specific period of the year if the vegetation is deciduous or semi-deciduous, or it may be constant throughout the year when

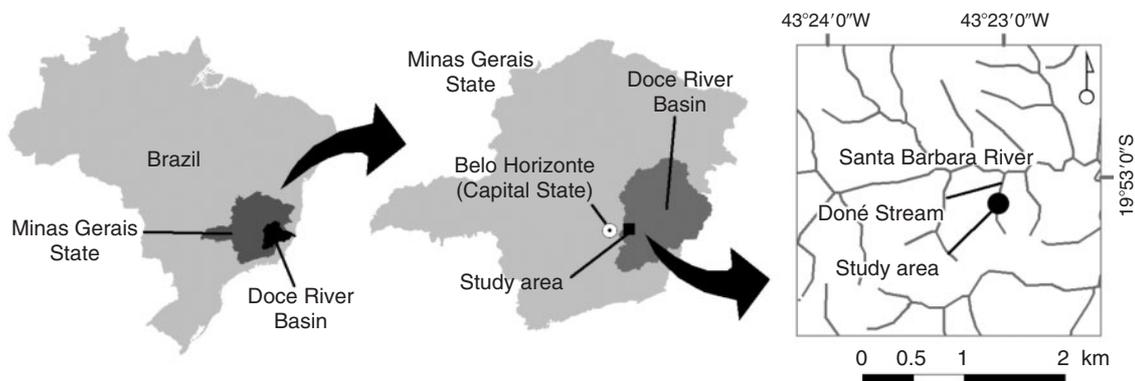


Fig. 1. Map of the study area, showing the location of Doné Stream in south-eastern Brazil.

the vegetation is perennial (Campbell *et al.* 1992). In tropical forests, the amount of detritus may show a seasonal distribution when there is a marked dry season (Williams-Linera and Tolome 1996), or it may be determined by a relatively constant input of plant matter throughout the year (Gonçalves *et al.* 2006a).

The organic matter originating from leaves, branches and reproductive structures is gradually reduced in size through processing by physical, chemical and biological agents (Royer and Minshall 2003). It is incorporated into the aquatic food web in the form of coarse particulate organic matter (CPOM), which is mainly composed of trunks, branches, leaves, fruits and flowers. Fine particulate organic matter (FPOM) originates from physical and chemical processes and from the action of micro- and macro-decomposers. The third form of organic matter is dissolved organic matter (DOM), which is composed of refractory chemical compounds (humic acids), products of the excretion of animals and algae, percolation and terrestrial lixiviation (Petersen and Cummins 1974; Allan 1995).

Several studies have examined the dynamics of organic matter in temperate streams (Poza *et al.* 1997; Wallace *et al.* 1997; Cillero *et al.* 1999; Molinero and Poza 2004; Swan and Palmer 2004; Reid *et al.* 2008). However, little information is available on organic-matter dynamics and its species composition in tropical streams (Angermeier and Karr 1984; Henry *et al.* 1994; Uieda and Kikuchi 1995; Afonso *et al.* 2000; Gonçalves *et al.* 2006a; Selva *et al.* 2007). On the basis of previous estimates of the riparian plant contribution in the Cerrado (Brazilian highland savanna) (Gonçalves *et al.* 2006a), we hypothesised that: (i) ~30% of riparian plant species contribute >70% of coarse particulate organic matter; and (ii) as tropical plant species are perennial and semi-deciduous, leaf fall would occur year round. The objectives of the present study were to evaluate the composition and structure of the plant species that colonise the riparian zone and to estimate seasonal variations in the terrestrial, lateral and vertical inputs of allochthonous organic matter and its benthic stock in a headwater stream located in a transition zone between the Atlantic Rain Forest and the Cerrado biomes.

Material and methods

Study area

The study was carried out in Doné Stream (19°53'59.5"S, 43°22'60.4"W), a tributary of the Santa Barbara River in

the middle portion of the Doce River basin in the state of Minas Gerais, south-eastern Brazil (Fig. 1). Doné Stream is located in an Atlantic Forest fragment (600 ha) in the Peti Conservation Unit managed by the Minas Gerais Electricity Company (CEMIG). This stream has warm water ($20.2 \pm 1.1^\circ\text{C}$, mean \pm s.d.), an acidic pH (6.15 ± 1.01), low electrical conductivity ($0.017 \pm 0.01 \text{ mS cm}^{-1}$), good oxygenation ($8.15 \pm 0.95 \text{ mg L}^{-1}$) and low turbidity ($15 \pm 6.05 \text{ NTU}$). The region is located in the eastern part of the Serra do Espinhaço mountain range, in a transition zone of the Atlantic Rain Forest and the Cerrado biomes, two of the five biodiversity hotspots in South America. The Cerrado is a periodically arid region where many plants invest in secreting cuticular waxes that reduce water loss from their leaves.

The climate of the study site is moderate, humid and subtropical (Cwb), with a well defined dry season from April to September, and a mean annual temperature of 21.7°C . The cumulative precipitation in the area during the study period was 703.3 mm. The highest rainfalls were recorded in November (261.5 mm) and December (275 mm), and the lowest rainfalls were recorded in June (0 mm) and July (3.1 mm). Doné Stream has well developed riparian vegetation, little human modification along its banks, a mean depth of $0.26 \pm 0.23 \text{ m}$, a mean width of $1.0 \pm 0.1 \text{ m}$ and a mean velocity of $0.53 \pm 0.17 \text{ m s}^{-1}$.

Methodology

The phytosociological characterisation was carried out using the Mueller-Dombois and Ellenberg (1974) method for $50 \text{ m} \times 10 \text{ m}$ (500 m^2) transects. All tree species, including individuals with a circumference at chest height (CCH) equal to or greater than 10.0 cm, were sampled (Meira-Neto and Martins 2000). Two plots parallel to the margins of the stream were established to sample the individuals that were responsible for the allochthonous organic matter contributions. The collected material was prepared for curation in a herbarium, following conventional techniques (Mori *et al.* 1989). The material was identified through comparative morphology, with the aid of a specialised bibliography and comparisons with material deposited at the herbarium of the Botany Department at the Universidade Federal de Viçosa (Vic.) and at the herbarium of the Centro Universitário do Leste (UNILESTE) de Minas Gerais (HUNL). After identification, all material was deposited

at the HUNL/UNILESTE. A species list was developed following the system in Cronquist (1988), except for specimens in the family Leguminosae where the system described in Polhill and Raven (1981) was used.

Sampling to evaluate the dynamics of the input of organic matter and stock was carried out monthly in a 50-m stretch of the river, over 9 months (April–December 2003). No sampling was carried out during January, February and March because the sampling nets were carried away by the stream current after heavy tropical storms.

The input of organic matter to the forest floor was evaluated by using four nets located on both banks under the riparian vegetation (1 m² each, 5-mm mesh size) at 15-m intervals. This sampling was carried out to estimate the potential stock of organic matter and the biomass that could reach the river indirectly (terrestrial input). The vertical input (organic matter that enters the stream directly) was evaluated by using 10 buckets (26 cm in diameter) suspended 2 m above the stream surface. The buckets had 3-mm holes in their bottoms to prevent water accumulation, and were anchored in a line across the stream from one bank to the other with synthetic ropes. The organic matter that entered the stream from the soil (lateral input) was evaluated using 10 nets (0.25 m² each, 5-mm mesh size) placed on the stream banks. The organic matter deposited on the streambed (benthic stock) was collected with a Surber sampler (0.0625 m²) to obtain three random samples each month. The organic matter accumulated in the buckets and nets was stored in previously labelled plastic bags for later processing in the laboratory.

All samples were dried, sorted and classified according to species composition. The CPOM was classified into three fractions: leaves, branches and others (fruits, flowers, seeds and debris). The samples were washed in the laboratory over a 1-mm mesh sieve to separate the CPOM (material retained on the sieve) from the fine particulates. Samples of CPOM were dried at 60°C for 72 h. All samples from the inputs and stock were weighed to the nearest 1 mg.

The first hypothesis was tested with a two-way ANOVA, using the compartments (different inputs and benthic standing stock) and time as factors to assess differences in the biomass of each plant species. Monthly differences among different compartments were tested with one-way ANOVA (second hypothesis), and differences among compartments were tested with one-way ANOVA. All data were log-transformed and checked for normality and homogeneity of variances (Zar 1996).

Results

Species composition

The phytosociological characterisation resulted in the identification of 99 specimens belonging to 60 genera and 33 families. The families with the highest number of species were Leguminosae (18 species), Myrtaceae (11 species), Annonaceae (eight species) and Euphorbiaceae (five species). Other families found in the study had only one or two representatives.

In the phytosociological survey, the species with the highest values of absolute density were *Pera glabrata* (Schott) Baill. and *Sloanea* sp. (19 individuals each), *Tapirira obtusa* (Benth.) Mitchell. (14 individuals), *Maprounea guianensis* Aubl. (11 individuals), *Hyptidendron asperrimum* (Spreng.) Harley

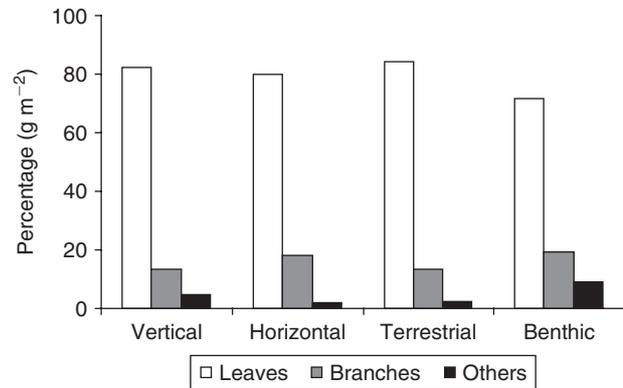


Fig. 2. Proportional total contribution of allochthonous organic matter to inputs (vertical, lateral and terrestrial) and benthic stock in a second-order reach of Doné Stream over the study period (April–December 2003).

and *Croton urucurana* Baill. (10 individuals each), with eight individuals of *Ocotea* sp. and *Emmotum acuminatum* (Benth.) Miers, which represented 30% of the species found. The other species found had fewer than five individuals each. With regard to the sum of the basal areas, *T. obtusa* had 0.18 m² ha⁻¹, *C. urucurana* had 0.14 m² ha⁻¹ and *Sclerolobium rugosum* Mart. had 0.13 m² ha⁻¹. One individual of *S. rugosum* had a 130-cm CCH and a total height of 19.2 m, and it alone contributed to the basal-area index for the species that was similar to the index obtained for the other two species that had 14 and 10 individuals respectively.

Dynamics of the organic matter

Leaves were the most abundant fraction of the organic-matter inputs and benthic stock. They represented 75% of the vertical input, 80% of the lateral input, 84% of the terrestrial input and 71% of the benthic stock (Fig. 2). Forty-four species were represented in the leaves found in the organic-matter inputs and stock in Doné Stream. However, seven species (16% of the total) represented >70% of the total input and benthic stock in the stream. The species with the highest relative biomass were *Tapirira obtusa* (23.2%), *Sclerolobium rugosum* (22.6%), *Croton urucurana* (7.6%), *Byrsonima* sp. (6.7%), *Inga* sp. (6.2%), *Hyptidendron asperrimum* (3.8%) and *Tapirira guianensis* Aubl. (2.7%) (Table 1). The contributions of the biomass of species to the terrestrial, vertical and lateral inputs and to the benthic stock were significantly different (ANOVA; $F_{92,1217} = 1.5$; $P = 0.003$). *Tapirira obtusa* and *C. urucurana* contributed most to the vertical input (Fig. 3a), *S. rugosum*, *T. obtusa* and *H. asperrimum* contributed most to the lateral input (Fig. 3b), *S. rugosum*, *T. guianensis* and *C. urucurana* contributed most to the terrestrial input (Fig. 3c) and *S. rugosum*, *T. obtusa* and *Inga* sp. contributed most to the benthic stock (Fig. 3d).

All organic-matter input categories (terrestrial, vertical and lateral) were represented throughout the entire study period (Fig. 4). However, inputs varied significantly among sampling months (ANOVA; $F_{8,81} = 10.5$, $P < 0.001$; $F_{8,80} = 4.9$, $P = 0.001$; $F_{8,26} = 5.1$, $P = 0.001$ respectively). There was no monthly variation in benthic stock (ANOVA; $F_{8,17} = 1.37$, $P = 0.3$). The highest biomasses for the vertical

Table 1. Mean monthly organic matter inputs (vertical ($n = 10$), lateral ($n = 10$) and terrestrial ($n = 4$) and benthic stock ($n = 3$) (g m^{-2} ; mean \pm s.e.) for each plant species in a second-order reach of Doné Stream over the study period (April–December 2003)

Species	Vertical input	Lateral input	Terrestrial input	Benthic stock
<i>Amaioua guianensis</i>	–	0.34 \pm 0.36	–	0.32 \pm 0.60
<i>Aniba firmula</i>	–	0.01 \pm 0.02	–	1.41 \pm 3.75
<i>Aparisthmium cordatum</i>	–	0.08 \pm 0.23	0.11 \pm 0.07	–
<i>Apuleia leiocarpa</i>	0.02 \pm 0.05	0.44 \pm 0.60	0.42 \pm 0.77	0.33 \pm 0.73
<i>Aspidosperma dispernum</i>	–	–	0.04 \pm 0.11	–
<i>Byrsonima</i> sp.	1.72 \pm 1.56	0.98 \pm 0.61	0.90 \pm 1.21	6.85 \pm 10.07
<i>Callisthene major</i>	–	0.01 \pm 0.02	0.01 \pm 0.01	0.06 \pm 0.14
<i>Callisthene</i> sp.	0.03 \pm 0.05	0.02 \pm 0.05	0.01 \pm 0.03	0.04 \pm 0.13
<i>Casearia</i> sp.	–	0.06 \pm 0.11	0.01 \pm 0.01	0.23 \pm 0.35
<i>Croton urucurana</i>	1.80 \pm 1.54	0.45 \pm 0.44	3.62 \pm 2.48	6.94 \pm 15.71
<i>Cupania emarginata</i>	0.01 \pm 0.04	0.25 \pm 0.19	0.21 \pm 0.25	1.36 \pm 1.20
<i>Cupania</i> sp.	0.04 \pm 0.13	0.37 \pm 0.21	0.54 \pm 0.58	0.05 \pm 0.14
<i>Daphnopsis</i> sp.	–	0.01 \pm 0.03	–	0.20 \pm 0.43
<i>Emmotum acuminatum</i>	–	0.06 \pm 0.17	–	–
<i>Eremanthus</i> sp.	–	–	0.01 \pm 0.01	1.12 \pm 2.08
<i>Guadua</i> sp.	0.02 \pm 0.03	0.20 \pm 0.10	0.11 \pm 0.13	0.57 \pm 0.51
<i>Himatanthus phagedaenicus</i>	–	0.01 \pm 0.04	0.16 \pm 0.22	0.06 \pm 0.18
<i>Hyptidendron asperrimum</i>	0.13 \pm 0.19	1.69 \pm 0.83	0.85 \pm 0.75	2.43 \pm 2.31
<i>Inga</i> sp.	1.97 \pm 1.78	0.07 \pm 0.10	0.73 \pm 0.58	8.00 \pm 5.94
<i>Kielmeyera altissima</i>	0.03 \pm 0.09	0.02 \pm 0.04	1.06 \pm 1.22	0.26 \pm 0.77
<i>Kielmeyera petiolaris</i>	–	0.08 \pm 0.14	–	–
<i>Kielmeyera</i> sp.	–	0.04 \pm 0.07	0.16 \pm 0.29	5.02 \pm 9.63
<i>Lacistema pubescens</i>	–	–0.10 \pm 0.10	0.07 \pm 0.15	–
Leguminosae sp. 1	2.41 \pm 1.61	1.08 \pm 0.54	1.04 \pm 1.18	2.75 \pm 2.77
Leguminosae sp. 2	–	–	0.01 \pm 0.01	0.01 \pm 0.02
Leguminosae sp. 3	0.25 \pm 0.23	0.73 \pm 0.53	1.64 \pm 3.00	0.36 \pm 0.73
<i>Licania spicata</i>	0.03 \pm 0.09	0.11 \pm 0.09	0.19 \pm 0.22	0.13 \pm 0.39
<i>Mabea fistulifera</i>	0.50 \pm 0.39	0.03 \pm 0.04	0.59 \pm 0.60	0.04 \pm 0.12
<i>Machaerium</i> sp.	–	0.02 \pm 0.03	0.07 \pm 0.16	0.04 \pm 0.13
<i>Machaerium villosum</i>	0.03 \pm 0.09	0.05 \pm 0.15	0.07 \pm 0.11	1.69 \pm 2.13
<i>Maprounea guianensis</i>	–	0.03 \pm 0.04	0.01 \pm 0.03	–
<i>Marlierea regeliana</i>	0.54 \pm 0.64	0.29 \pm 0.29	0.44 \pm 0.52	0.24 \pm 0.72
Melastomataceae sp.	0.01 \pm 0.03	–	–	1.22 \pm 2.89
Myrtaceae sp.	–	0.86 \pm 0.49	0.18 \pm 0.15	0.84 \pm 1.14
<i>Ocotea</i> sp.	–	0.04 \pm 0.05	0.06 \pm 0.10	0.07 \pm 0.20
<i>Pera glabrata</i>	–	0.05 \pm 0.08	0.10 \pm 0.19	0.05 \pm 0.14
Pteridophyta	–	0.01 \pm 0.01	0.05 \pm 0.11	1.07 \pm 2.05
<i>Rapanea umbelata</i>	0.09 \pm 0.20	–	0.09 \pm 0.12	0.53 \pm 1.07
<i>Sclerobium rugosum</i>	0.79 \pm 1.51	5.02 \pm 2.31	8.56 \pm 7.34	26.75 \pm 22.34
<i>Sloanea</i> sp.	0.11 \pm 0.24	0.05 \pm 0.09	–	0.13 \pm 0.38
<i>Tapirira guianensis</i>	0.43 \pm 0.61	0.06 \pm 0.07	3.73 \pm 7.11	0.39 \pm 0.73
<i>Tapirira obtusa</i>	12.11 \pm 6.07	3.71 \pm 2.63	0.51 \pm 0.63	10.74 \pm 8.75
<i>Tovomitopsis paniculata</i>	0.10 \pm 0.29	0.14 \pm 0.16	0.23 \pm 0.33	0.14 \pm 0.42
<i>Xylopia sericea</i>	–	0.03 \pm 0.09	0.04 \pm 0.08	0.22 \pm 0.46

(64.2 \pm 9.7 g m^{-2}) and lateral inputs (50.1 \pm 7.2 g m^{-2}) were recorded in November, whereas the highest biomass for the terrestrial input (83.3 \pm 18.4 g m^{-2}) was recorded in October 2003 (Fig. 4a–c). The benthic stock showed high plant biomass compared with the inputs, with the highest values observed in December (362.6 \pm 236.4 g m^{-2} ; Fig. 4d). All input categories (vertical, terrestrial and lateral) and benthic stocks were significantly different from each other (ANOVA; $F_{3,23} = 44.4$, $P = 0.001$). Significantly higher biomass values were found in the benthic stock than with the terrestrial, vertical and lateral inputs, in both the monthly means (Fig. 5).

Discussion

Effect of the composition of the riparian species

The most important plant species found in the riparian zone of Doné Stream differed in their occurrence and their ecological grouping. This stream valley contains several plant species that are typical of secondary forest and regenerating forest formations. *Tapirira obtusa* occurs in areas characterised as ‘Cerrado’ and also in tropical rainforests, and is considered to be a climax species (Pinto *et al.* 2005; Brito *et al.* 2006). *Sclerobium rugosum* is a secondary forest indicator, and is a pioneer species

<i>Byrsonima</i> sp.	18.7
<i>Croton urucurana</i>	20.2
<i>Inga</i> sp.	21.9
<i>Sclerolobium rugosum</i>	8.6
<i>Tapirira obtusa</i>	133.1

<i>Byrsonima</i> sp.	10
<i>Croton urucurana</i>	4.9
<i>Inga</i> sp.	0.8
<i>Sclerolobium rugosum</i>	54.5
<i>Tapirira obtusa</i>	39.9

<i>Byrsonima</i> sp.	10.1
<i>Croton urucurana</i>	38.6
<i>Inga</i> sp.	7.4
<i>Sclerolobium rugosum</i>	91.8
<i>Tapirira obtusa</i>	5.8

<i>Byrsonima</i> sp.	51.2
<i>Croton urucurana</i>	50.7
<i>Inga</i> sp.	61.4
<i>Sclerolobium rugosum</i>	209.2
<i>Tapirira obtusa</i>	83.1

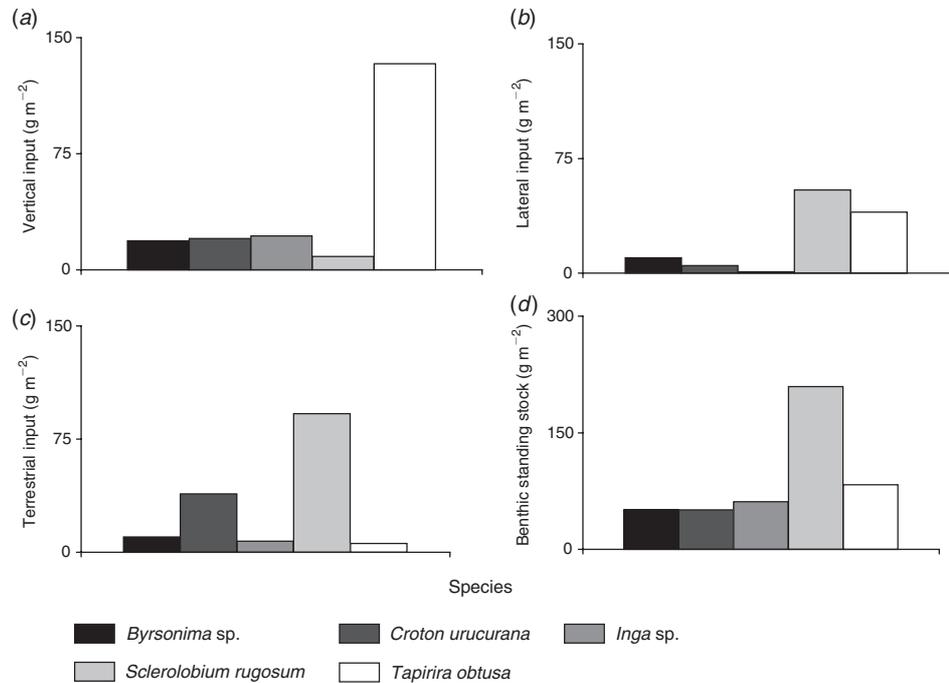


Fig. 3. Total contribution of the main species found in the different organic-matter categories: (a) vertical input, (b) lateral input, (c) terrestrial input and (d) benthic stock in a second-order reach of Doné Stream over the study period (April–December 2003).

that occurs during the initial stages of plant succession (Pinto *et al.* 2005). *Tapirira guianensis* is conspicuous because of its high density and frequency in the tree and regenerative strata of all headwater categories. It occurs both in riparian vegetation and in Cerrado areas (Sano and Almeida 1998; Oliveira-Filho and Ratter 2001). *Croton urucurana* ('sangra d'água') is typical of regenerating riparian forests. It is a pioneer species that contributes by improving soil conditions so that other species are able to colonise and establish (Catharino 1989). *Byrsonima* sp. and *Inga* sp. are secondary forest pioneer species. *Inga* spp. can develop in both flooded and well drained areas, and can be used for the recovery of degraded areas (Almeida *et al.* 1998). *Hyptidendron asperrimum* is also an indicator of secondary forest formations, and occurs in both riparian zones and in dry forests (Sano and Almeida 1998). This composition of the riparian zone indicates that, in the past, the riparian vegetation of Doné Stream was subject to human influence, and is now secondary vegetation. The occurrence of these species emphasises the importance of the Peti Conservation Unit as a fragment of semi-deciduous vegetation in a region that is heavily exploited for iron mining. We believe that the past human influence explains the low number of species (seven, 16% of the total) that contributed >70% of the allochthonous organic matter, and thus reject our first hypothesis.

Dynamics of the organic matter

The peaks of allochthonous biomass input into temperate ecosystems occur during autumn (October through to December) when the deciduous species lose their leaves (Molinerio and Pozo 2004). In our study, an increase in the vertical and terrestrial inputs of allochthonous organic matter was observed at the end

of the dry period (winter) and at the beginning of spring. This result corroborates the findings of Henry *et al.* (1994) and Selva *et al.* (2007), who observed the highest input of organic matter during September and October (in Atlantic Rain Forest) and in February through to April (Amazon Forest) at the outset of the dry season. The hydric stress of riparian forest plants after a long dry period must be the trigger for the higher input of organic matter. As a result of the action of the ethylene produced, some plants lose their leaves to avoid excessive water loss from transpiration (Taiz and Zeiger 2004). We rejected our second hypothesis because there was a tendency for seasonal input of CPOM.

The high values found for the vertical and terrestrial inputs are attributed to the fall of leaves from the riparian trees and to the wind and strong storms that can provide large quantities of plant matter to lotic ecosystems (Afonso *et al.* 2000; Selva *et al.* 2007). The present results highlight the importance of terrestrial organic-matter input and its transfer to this stream located in a semi-deciduous Atlantic Rain Forest fragment. Previous studies of the riparian vegetation of the high-altitude Indaiá Stream in the Cerrado (Gonçalves *et al.* 2006a) and Amazon catchment (Selva *et al.* 2007) have also highlighted the influence of terrestrial input in the dynamics of allochthonous organic matter.

Our estimates differ from those obtained by Gonçalves *et al.* (2006a) because the estimated inputs were higher for Doné Stream, whereas the estimated stock values were higher for Indaiá Stream. Both streams are similar in their hydraulic and physical dimensions. A possible explanation is the differences in composition, organisation and densities of the trees in the riparian zones of these streams (Fleituch 2001). In addition, Indaiá Stream is located in a rupestrian field region, where the leaves of the plants decompose slowly because of the presence of

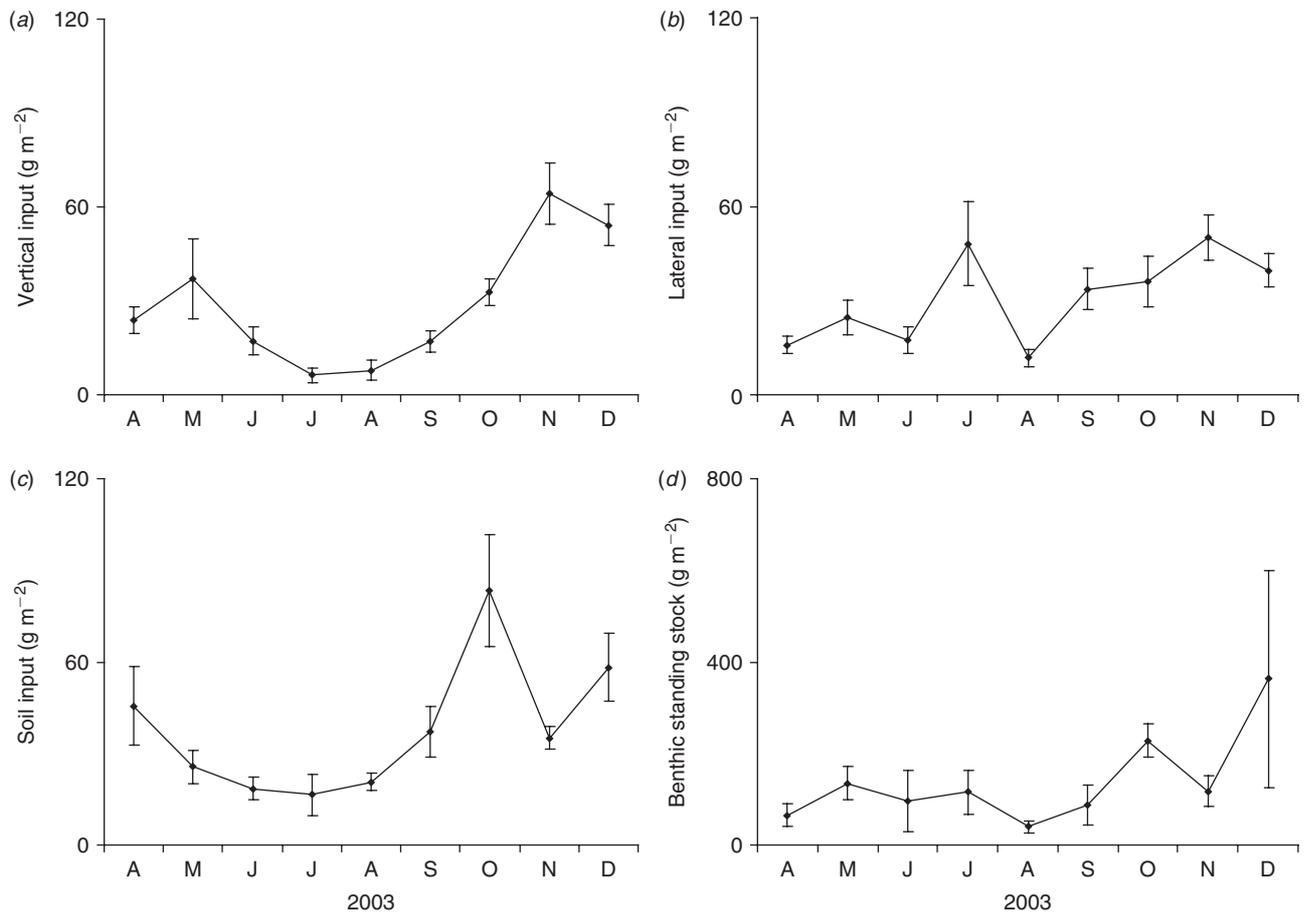


Fig. 4. (a) Vertical input, (b) lateral input, (c) terrestrial input and (d) benthic stock estimated during the sampling period (mean ± s.e.) in a second-order reach of Doné Stream over the study period (April–December 2003).

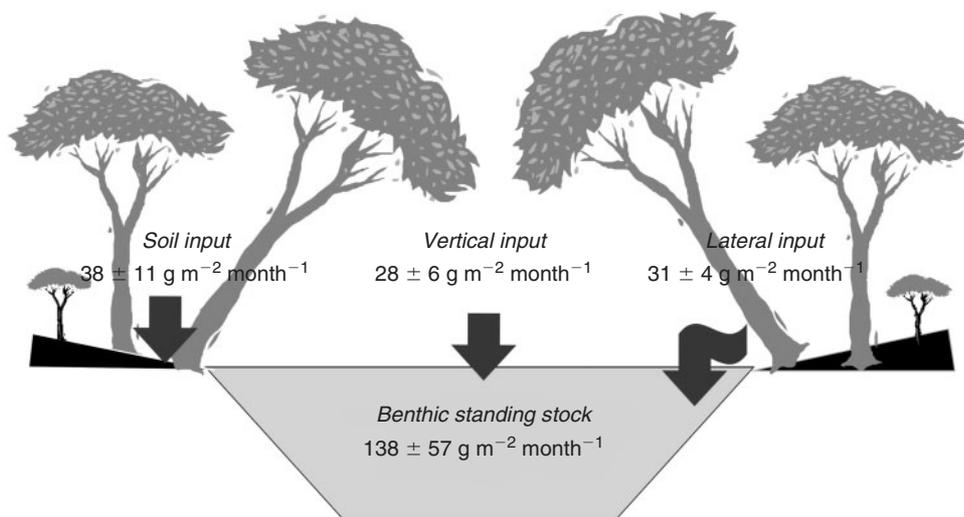


Fig. 5. Estimated biomass of inputs (vertical ($n = 10$), lateral ($n = 10$) and terrestrial ($n = 4$)) and benthic stock ($n = 3$) over 9 months (mean ± s.e.) in a second-order reach of Doné Stream over the study period (April–December 2003).

wax (Gonçalves *et al.* 2006a, 2006b). In contrast, Doné Stream is located within an Atlantic Rain Forest fragment (high density of plant species, with rapid decomposition) (Moulton and Magalhães 2003). Consequently, the nature of the plant detritus would be the determining factor for the different decomposition rates. The slower leaf-breakdown rate facilitates the higher accumulation rate in the benthic stock. Other explanatory factors could be differences in stream velocity and discharge, which are considerably lower in the Indaiá Stream than in the Doné Stream.

Leaves were the most abundant fraction in the composition of the input and stocked organic matter, as observed in other studies in temperate (Cillero *et al.* 1999; Swan and Palmer 2004; Reid *et al.* 2008) and tropical ecosystems (Henry *et al.* 1994; Gonçalves *et al.* 2006a). The composition of the litter fraction did not vary seasonally; leaves were the main fraction during all months. In contrast, Molinero and Pozo (2004) found, in a temperate region, that different fractions of plant detritus varied according to the different times of the year. Most plants found in temperate regions are deciduous, whereas in tropical regions most species are evergreen. The large amount of leaves produced by the riparian vegetation indicates that leaves are the main component of allochthonous organic matter input and are the main energy source for heterotrophic aquatic organisms (Webster *et al.* 1999).

The continuous contribution of the terrestrial, vertical and lateral inputs to Doné Stream is probably related to the morphological characteristics of the locality (e.g. slope and bank stability, soil type, vegetation age) that might influence the direction and the amount of allochthonous organic matter stock in the streambed (Maridet *et al.* 1995; Fleituch 2001). A study by Cillero *et al.* (1999) quantified the vertical and terrestrial inputs and found that both showed similar annual values in a stream in north-western Spain because they represent the material that falls directly into the stream and onto the ground. In the present study in Doné Stream, the terrestrial input was larger than the vertical input, which resulted in a larger lateral contribution. For this reason, our results contradict the results of previous studies that have shown that vertical input contributes the most organic matter to watercourses (Pozo *et al.* 1997; Wallace *et al.* 1997; Cillero *et al.* 1999). This result indicates that the higher input probably results from the morphology of the riverbanks. For example, riverbanks in some sections of our study reach in Doné Stream had slopes that exceeded 60°. This steep slope favours the entrance of organic matter into the stream. Lateral input may be reduced by the presence of dense shrubs that retain the leaves before they enter the river (Molinero and Pozo 2004) or may be increased by factors such as the slope of the bank and rain and wind action (Webster *et al.* 1995). The lateral input can represent 70% of the total plant material entering the system in open areas, or >50% in streams where marginal vegetation is well developed or protected from the wind by mountains (Cushing 1997). Differences in the amount of plant biomass in the lateral input reflect differences in the composition of the arboreal and shrub species distributed in the riparian vegetation. The organic-matter contribution of riparian vegetation to streams is greater when the vegetation is mainly arboreal than when the dominant vegetation is herbaceous (Henry *et al.* 1994).

In comparison with the results of other studies carried out in streams in tropical regions, our estimates of vertical inputs

were generally lower in Doné Stream (e.g. Henry *et al.* 1994; Uieda and Kikuchi 1995; Afonso *et al.* 2000). However, the value reported in the present study is similar to those found in temperate regions (Wallace *et al.* 1997; Molinero and Pozo 2004). In contrast, studies carried out in temperate (Pozo *et al.* 1997; Wallace *et al.* 1997; Molinero and Pozo 2004; Swan and Palmer 2004) and in tropical regions (Henry *et al.* 1994; Afonso *et al.* 2000; Gonçalves *et al.* 2006a) have estimated lower lateral inputs than vertical inputs, in contrast to our findings for Doné Stream. In addition, in some months the lateral input was higher than the terrestrial input, probably because there were large amounts of organic material accumulated on the ground. Because not all of the material that falls on the ground reaches the stream immediately, during some parts of the year factors such as winds, rain and floods may influence lateral transport from the ground into the stream (Vannote *et al.* 1980; Pozo *et al.* 1997).

Benthic stocks were higher than inputs because this value accounts for all of the material received from the different input categories (vertical and lateral) as well as for materials transported from upstream reaches. In addition, headwater streams may have high retention capacities, being able to retain (over distances of up to 67 m) almost 90% of the leaves that enter the watercourse (Canhoto and Graça 1998). The stream order and discharge and the riparian vegetation characteristics, such as litter type, are determining factors for the retention capacity of leaves (Webster *et al.* 1994; Pozo *et al.* 1997). In general, materials that can be retained for over 4 months have slower decomposition rates, and thus contribute to organic-matter stocks over time (Gonçalves *et al.* 2006b; Moretti *et al.* 2007; all in the Cerrado).

The assessment of the contribution of each riparian plant species to the composition and amount of allochthonous CPOM is of paramount importance for understanding the close relationship between the riparian zone and the fresh-water ecosystem (Wantzen *et al.* 2008). Furthermore, it is the basis for the identification of the key plant species for the energy flux and nutrient cycling in tropical headwaters. The rejection of our first hypothesis suggests the importance of studying organic-matter dynamics to assess the ecological effects of human activities on riparian zones.

Because there is little information about organic-matter dynamics in tropical riparian zones, we propose three main questions for future studies: (1) do riparian zones in transition biomes have few key plant species in their organic-matter dynamics; (2) do tropical riparian zones, with a high richness of plant species, have few dominant species (low evenness) because of competition for nutrients; and (3) what ecological processes (e.g. ecosystem productivity, decomposition, nutrient cycling) are more affected by changes to riparian communities, such as the removal or replacement of native species?

In the present study, the results indicated that there was an increase in the amount of organic matter entering the terrestrial and aquatic ecosystems at the end of the dry period, rejecting our second hypothesis. This result corroborates a possible seasonal energy input in Brazilian Cerrado headwater streams (Wantzen *et al.* 2008). There is still a lack of information about the influence of this seasonality on stream functioning because the timing of leaf loss in tropical riparian forests is more variable and may reflect a response to water scarcity and soil-nutrient limitations.

The study of organic-matter dynamics in riparian zones in headwater streams is important for understanding the functioning of catchments, based on the importance of each plant species to terrestrial and aquatic ecosystems. Moreover, studies on protected areas may support restoration interventions and the revitalisation of streams in heavily forested catchments in Neotropical regions, where anthropogenic disturbances are a major force driving the degradation of these systems.

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