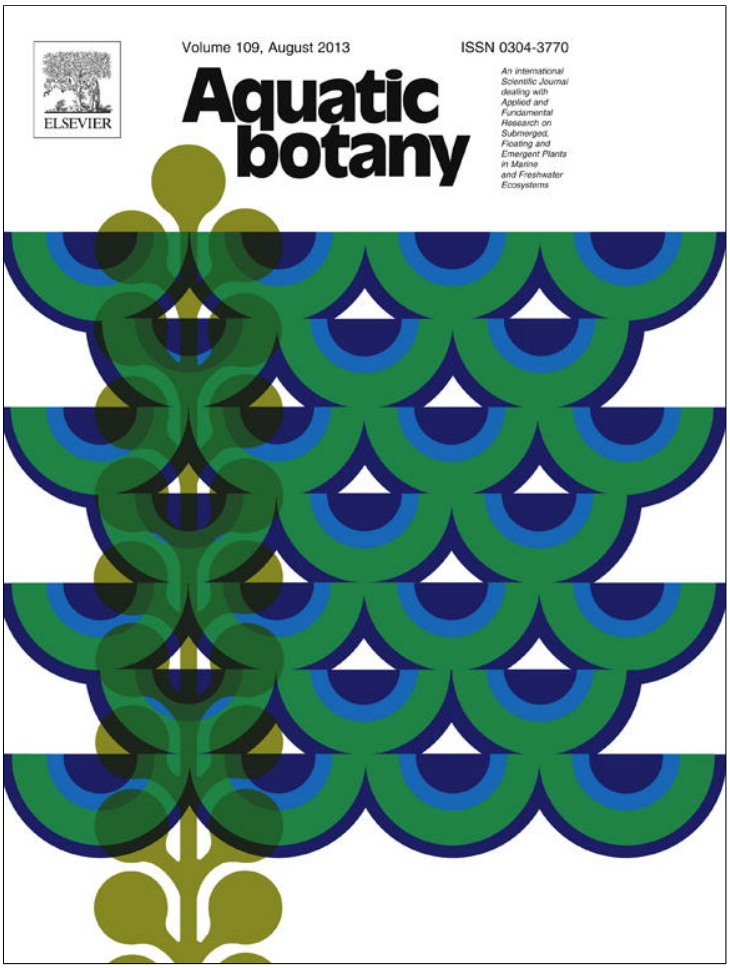

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# Organic-matter dynamics in the riparian zone of a tropical headwater stream in Southern Brasil

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ABSTRACT

We assessed the dynamics of allochthonous coarse particulate organic matter (CPOM) in a tropical headwater stream in the foothills of the Ouro Branco Sierra (S. Brazil; at 1300 m a.s.l.) over a yearly cycle, and the contribution of leaves, twigs, and other plant parts to the different types of input and stock. Additionally, we identified the key species that contribute to each type of input and to seasonal patterns in the input and storage of CPOM (particles > 1.00 mm). Our study tested (and rejected) the hypothesis that the majority of riparian plant species along tropical headwater streams are perennial, and therefore the input of CPOM tends to be continuous over the course of the year. Leaves contributed 74% of CPOM, with input increasing toward the end of the dry season (September to October). Of the total of 188 plant species identified in the riparian zone, 47 species together contributed over 28% of the detritus to the aquatic ecosystem. The species that contributed most were *Protium* spp., *Cabralea canjerana* (Vell.) Mart., and *Casearia decandra* Jacq. The CPOM dynamics of Garcia Stream showed a highly seasonal pattern due to the influence of precipitation. A number of species characteristic of the Amazon and Atlantic Rain forests were identified, together with species of the Cerrado, indicating that the riparian vegetation should not be considered part of a single forest domain, but rather a unique and integrated system that functions as an ecological corridor for species dispersal. The data obtained here confirmed the ecological complexity of the riparian tropical system, derived from the diversity of plant species and the seasonal dynamics of CPOM, related to the phenology of the plant community.



## 1. Introduction

The riparian zone is considered an important interface between aquatic and terrestrial ecosystems (Naiman et al., 2005). Riparian zones perform a number of hydrological functions that sustain the environmental integrity of catchments and their streams, such as buffering and filtering agricultural nutrients and pollutants, and controlling sedimentation and erosion (Verhoeven et al., 2006). Conservation of riparian vegetation increases water-storage capacity while maintaining the original quality of the aquatic environment (Vondracek et al., 2005; Vandermeer and Perfecto, 2007). Riparian vegetation supplies and accumulates organic matter, stabilizes stream banks, and increases the heterogeneity of the riverbed, resulting in different current speeds and sediments, and a variety of habitats for biological communities (Naiman et al., 2005). In low-order streams, the canopy may cover 80–100% of the watercourse (Rheinhardt et al., 2012), buffering streams against wide fluctuations in temperature (Lima and Zakia, 2001). Riparian vegetation also constitutes an important corridor for animal migration, and thus contributes to the maintenance of faunal diversity (Becker et al., 2007, 2010) and plant dispersal (Méio et al., 2003).

The organic matter (OM) derived from riparian vegetation is an important source of energy for low-order streams, especially those that are relatively shaded (Weigelhofer and Waringer, 1994), where the lower light penetration may limit primary production by aquatic organisms (Mosisch et al., 2001). This allochthonous OM connects the terrestrial and aquatic ecosystems, and contributes importantly to the secondary productivity of streams (Odum and Barrett, 2005), and has been studied by investigating the breakdown of coarse particulate organic matter (CPOM). OM may enter streams from the forest canopy (Weigelhofer and Waringer, 1994), or indirectly by rainfall draining through the soil (Dudgeon, 1993). Seasonal variation in plant productivity generally determines the quantity and quality of allochthonous OM in low-order streams, and the patterns of its processing and retention (Weigelhofer and Waringer, 1994; Magana, 2001).

In temperate deciduous forests, leaf fall is closely linked to seasonal climatic variation, mainly in autumn (Stout, 1980; Delong and Brusven, 1994; Dodds, 2002; Artmann et al., 2003). In many tropical

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areas, litter fall occurs mainly in the dry season (Morellato, 1992; Antunes and Ribeiro, 1999). Some published information on litterfall patterns in tropical systems is available (e.g., Henry et al., 1994; Afonso et al., 2000; Gonçalves et al., 2006a; França et al., 2009).

In the tropics, leaf fall is a response to hydric stress, and the loss of leaves is a strategy to reduce water loss through transpiration during the driest period of the year (França et al., 2009). In temperate regions, abscission is stimulated by lower temperature and light, and the loss of leaves reduces heat loss and prevents the accumulation of snow and ice (Naiman et al., 2005). On the Iberian Peninsula, summers are hot and dry, and precede the input of CPOM in the autumn (Diez et al., 2001). In Austria, Artmann et al. (2003) recorded peaks of input in a temperate stream in winter and spring, related to precipitation and the relatively harsh weather in those seasons. In Kenya, Magana (2001) found a negative correlation between the production of CPOM derived from leaves and precipitation levels. However, the contribution of twigs is related positively to rainfall (Elosegi et al., 2007). Based on the above, we assumed that: (i) headwater streams function as hotspots of biodiversity by transforming OM from terrestrial systems (Sabater et al., 2008); (ii) there is a need for a reliable data base to support the development of conservation and management strategies for tropical watersheds; (iii) low-order streams are dependent on allochthonous OM. We tested the hypothesis that because the majority of riparian species in tropical headwater streams are perennial, the input of OM will tend to be constant over the course of the year. Our aims were to (i) assess the temporal dynamics of allochthonous CPOM (>1.00 mm) in a tropical low-order stream during a yearly cycle; (ii) evaluate the contribution of leaves, branches and other plant parts to litter standing stock; and (iii) identify the species that contributed the most litter.

## 2. Material and methods

### 2.1. Study area

This study was conducted along the Garcia Stream, a third-order tropical stream (1300 m a.s.l., $0.23 \pm 0.12\ m^3\ s^{-1}$ water flow) in southeastern Brazil (20°21′S, 43°41′W). The surrounding vegetation is composed of high-altitude Brazilian rupestrian fields (Carvalho et al., 2012), and pastures and forest fragments of differing sizes on local farms. The tropical highland (Cwb) climate has a marked seasonal variation in temperature (between 13 °C and 22 °C; annual mean 17 °C), and precipitation (approximately 1200 mm, October–April). The foothills of the Ouro Branco range are dominated by broadleaf rainforest typical of the Atlantic Rain Forest, but the vegetation shifts to the typical Cerrado and then mountain rock fields with gallery forests as the altitude increases from 800 to 1500 m a.s.l.

### 2.2. Experimental design

#### 2.2.1. Botanical Inventory

Sets of 28 plots of 10 m × 20 m along a 200-m reach were established along both banks of Garcia Stream, representing a total area of 0.56 ha of vegetation. Within each plot, all trees with a circumference at breast height (1.30 m) of at least 15 cm were identified and counted. Voucher specimens were deposited at the UNILESTE herbarium (HUNL) in Minas Gerais. The online collection of the New York Botanical Garden (http://sciweb.nybg.org) was consulted to confirm the habitat of the species identified. All species and synonyms, and their respective authors, were confirmed and updated, where necessary, by consulting the sites of the Missouri Botanical Garden (www.mobot.org) and the Lista de Espécies da Flora do Brasil (www.floradobrasil.jb.gov.br).

We studied the organic-matter dynamics as the qualitative and quantitative evaluation of the material that enters the aquatic ecosystem through (1) direct, or vertical input from the vegetation overhanging the stream; (2) indirect, or horizontal input from the soil to the stream, resulting from runoff, winds, and animal movements; (3) terrestrial input, derived from the leaf litter, which represents the potential stock that can be transported to the stream, and contributes to the understanding of phenological patterns; and (4) the benthic stock, i.e., the OM accumulated on and in the stream bottom, which is influenced directly by the flow of water and the morphology of the streambed (Elosegi and Pozo, 2005; Gonçalves et al., 2006a).

CPOM (>1.00 mm) was collected from the riparian ecosystem, for the whole of each month from May 2004 to April 2005. Vertical input (VI) was estimated using 10 buckets, 26 cm in diameter with holes in the bottom to drain off excess water. A cord from a tree suspended the buckets, 2 m above the streambed. Horizontal input (HI) of partially decomposed leaves was evaluated using ten nets with an opening of 0.1 $m^2$ (0.2 m high by 0.5 m wide; 1 mm mesh size), which were installed along both banks in the stream (five on each bank) at 10-m intervals. Terrestrial input (TI) of fresh recent leaves was measured using six 1 $m^2$ nets with a 10-cm edge (three on each bank) suspended 1 m above the ground, distributed randomly at 10-m intervals (1 mm mesh size). Samples of the benthic OM stock (BS) were collected using a 0.1 $m^2$ Surber sampler with a 250 μm mesh (after the material was washed on a sieve of 1 mm mesh size). Five replicates were distributed along the stream at a minimum interval of 10 m. Samples were transported to the laboratory for drying, weighing, and processing.

#### 2.2.2. Laboratory analyses

In the laboratory, the specimens were dried in an oven at 60 °C for 72 h to constant weight. They were then sorted into reproductive (flowers, fruit) and vegetative (twigs, leaves) material, and weighed (±0.1 g DW). Leaves were sorted by species, identified by comparison with voucher specimens, and weighed separately.

#### 2.2.3. Data analysis

The differences in values of CPOM (dependent variable) among compartments (VI, HI and TI; categorical variables) were tested using Repeated Measures two factorial analysis of variance (RM-ANOVA), which were assessed as a function of time (continuous variable). We distinguished the benthic stock of the inputs (VI, HI, TI). Data normality was tested according to Kolmogorov–Smirnov, and the data were transformed whenever necessary with the neperian logarithm (ln). When the time variable was statistically different, the differences between each sampling time were determined from the contrast analysis ($p < 0.05$) (Crawley, 2007).

For the analysis of the role of the plant species in the allochthonous CPOM input and benthic stock, only species with an annual contribution of more than 1.0 g DW $m^{-2}$ were included. Based on this criterion, 90 species were selected for indicator species analysis (Dufrêne and Legendre, 1997), which provides an Indicator Value (IV) for the plant species importance in the riparian composition from 0, for a non-indicator, to 100, for a perfect indicator. This analysis was based on the frequency and CPOM of the assigned species. The significance of the value was analyzed using a Monte Carlo test with 10,000 permutations, and only the significant values ($p < 0.05$) are presented here.

The structure of the plant community by total input of leaves was tested by a MANOVA/Pillai Trace test, between the compartment, time and interaction between these factors, and when the analyses showed significant effects of the treatments, means were compared using contrast analyses ($p < 0.05$). MANOVA can be used when multiple dependent variables show interdependence (Scheiner, 2001). For the MANOVA, we used the sequential

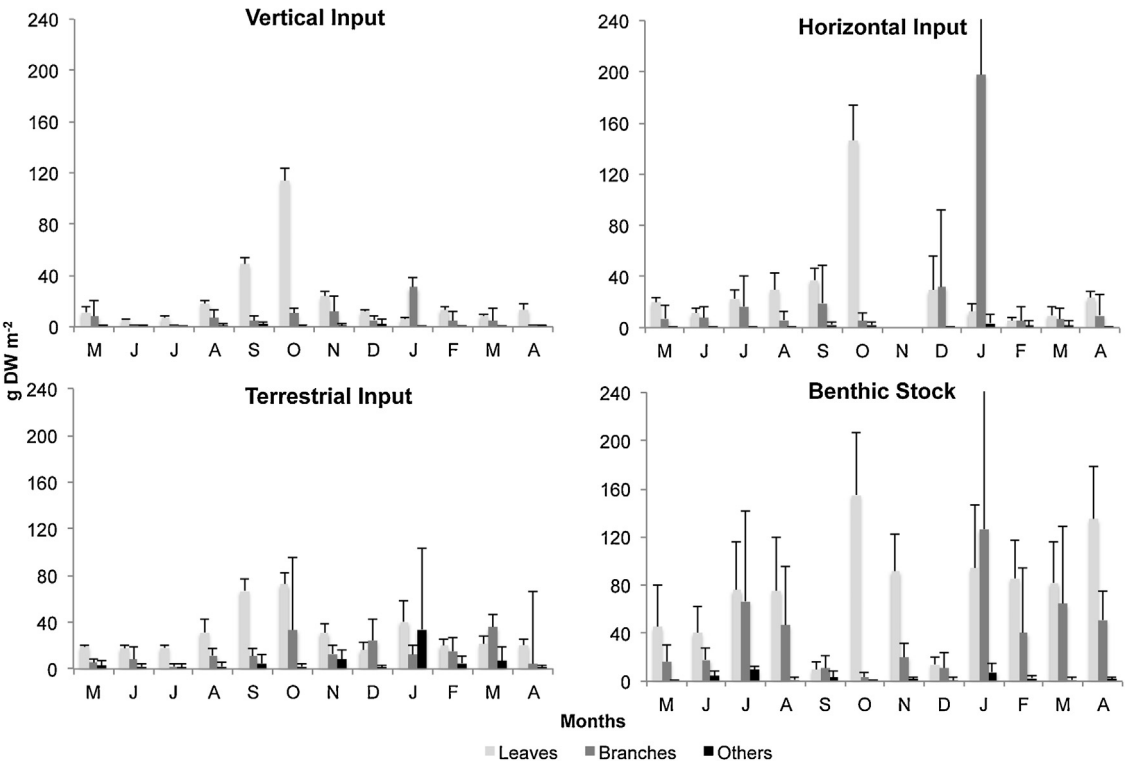


**Fig. 1.** Contribution of the different categories of CPOM (mean and standard deviation of monthly means among the plots) in Garcia Stream between May 2004 and April 2005.

Bonferroni correction for multiple comparisons/adjustments (Rice, 1989). All analyses were performed in the program R (R Development Core Team, 2008).

## 3. Results

### 3.1. Organic matter dynamics

Leaves contributed 74% of the total CPOM over the study period, corresponding to around 73% of the vertical input, 75% of the horizontal input, and 60% of the terrestrial input, with increased leaf fall in September and October (Fig. 1). The benthic stock of leaves was around 37% in most months. The contribution of branches and other plant parts was highest in July (67 g DW $m^{-2}$ and 9 g DW $m^{-2}$, respectively) and January (126 g DW $m^{-2}$ and 8 g DW $m^{-2}$, respectively).

Between October and April, the rainy season, precipitation ranged from 75 mm to 180 mm. In the remaining months of the study period, the dry season, precipitation ranged from 0 mm in August and September to 38 mm in May. The vertical and terrestrial input of foliar CPOM was greatest during the dry season, reaching a maximum of 187 g DW $m^{-2}$ in October, while the lowest input was recorded in June (23 g DW $m^{-2}$; Fig. 2).

The mean annual budgets of leaves in the horizontal (HI; 382 g DW $m^{-2}$ $year^{-1}$, $36 \pm 58$ g DW $m^{-2}$ $month^{-1}$), terrestrial (TI; 337 g DW $m^{-2}$ $year^{-1}$, $28 \pm 49$ g DW $m^{-2}$ $month^{-1}$) and vertical (VI; 302 g DW $m^{-2}$ $year^{-1}$, $25 \pm 35$ g DW $m^{-2}$ $month^{-1}$) inputs were significantly different. The TI reached its maximum levels in September and October (70 g DW $m^{-2}$ and 75 g DW $m^{-2}$, respectively), VI (48 and 113 g $m^{-2}$) and HI (37 and 146 g DW $m^{-2}$; Table 1 and Fig. 1). The benthic stock was 483 g DW $m^{-2}$ $year^{-1}$ and $40 \pm 66$ g DW $m^{-2}$ $month^{-1}$. When we assessed the monthly variation, the BS showed the highest values in October, January, and April (ANOVA, $F_{11,38} = 3.1$; $p = 0.001$), reaching a maximum of 155 g DW $m^{-2}$ in October (Fig. 1).

### 3.2. Plant composition of the riparian zone and litter inputs

We identified 1258 individuals belonging to 192 species, in 90 genera and 52 families. The families with the largest numbers of species were Myrtaceae (29 species), Lauraceae (21), Leguminosae-Caesalpinioideae (8), and Euphorbiaceae (8). The other families comprised less than 5% of the total species.

One hundred and eighty-eight species were present in the leaf litter, and 83 of them were identified through comparison with available specimens. The leaf litter was very heterogeneous in plant composition in each compartment studied and the time (Table 1). The most common and important leaf species in the riparian zone (identified by indicator-species analysis) were *Protium* spp., *Cabralea canjerana* (Vell.) Mart., *Machaerium nyctitans*,

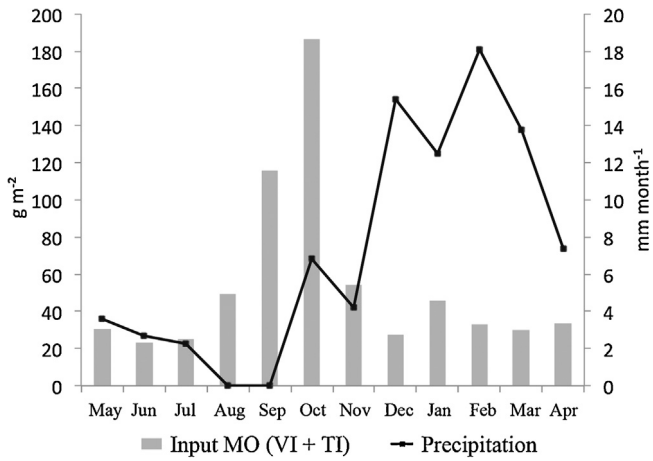


**Fig. 2.** Relationship between monthly means of precipitation and CPOM inputs (mean vertical input + mean terrestrial input) in Garcia Stream between May 2004 and April 2005.

**Table 1**
Results of statistical analyses of total CPOM and contribution of leaf species of the riparian plant community among compartments (vertical, terrestrial and horizontal inputs) and sample time (months) on the Garcia Stream from May 2004 to April 2005.

| Statistical analyses | Freedom degree | % Sum square | *F* | *p* |
|---|---|---|---|---|
| RM-ANOVA | | | | |
| Compartments | 2 | 8 | 14.2 | <0.001 |
| Residuals | 23 | 6 | | |
| Error: Within | | | | |
| Months | 11 | 37 | 25.4 | <0.001 |
| Compartments × Months | 22 | 16 | 5.7 | <0.001 |
| Residuals | 253 | 33 | | |
| | | Pillai's trace test | | |
| MANOVA (plant species community) | | | | |
| Intercept | 186 | 0.107 | 7.6 | |
| Compartments | 558 | 0.012 | 3.0 | <0.001 |
| Months | 186 | 0.108 | 7.5 | <0.001 |
| Compartments × Months | 558 | 0.015 | 2.7 | <0.001 |

*Guettarda virbunoides* Cham. & Schltdl., *Casearia decandra* Jacq., and *Clethra scabra* Pers. Altogether, 47 of the riparian species (57% of the species identified) contributed 28% of the mean CPOM of leaves (Supplementary Material).

*Protium* spp. was the most common genus (8% – Vertical Input; 29% – Lateral Input; 4% – Terrestrial Input; 4% – Benthic Stock). The indicator-species analysis identified 15 species in VI, of which the most abundant were Species No. 33 (6%), *G. virbunoides* (5%), *C. scabra* (4%), *M. nyctitans* (4%), and *C. canjerana* (3%). In the horizontal input we found 28 species, of which the most abundant were *C. canjerana* (5%), *C. scabra*, Species No. 82 (4%), and *Sclerolobium rugosum* (3%). Of the 16 species that were important in the terrestrial input, the most prominent were *S. rugosum* Mart. (11%), *Kielmeyera albopunctata* Saddi., *C. canjerana* (Vell.) Mart. (3%), and *C. scabra* Pers. (2%). In the benthic stock we found only seven species, mainly *S. rugosum* Mart. (5%), Species No. 33, and *Lamanonia tervata* (4%). The monthly contribution of some species, e.g., *C. canjerana*, was relatively important during both the rainy and dry seasons (Table 1 and Supplementary Material). Other species contributed relatively minor amounts overall, but became significant in months of reduced leaf fall, e.g., *Vismia brasiliensis* Choisy, which peaked in April.

Nineteen of the 37 species that contributed significantly to the inputs were identified as more-important species in the organic-matter dynamics of the study area (Supplementary Material). *Guatteria sellowiana* Schltdl., *Nectandra* sp. Rol. ex Rottb., *G. virbunoides* Cham. & Schltdl., *C. decandra* Jacq., and *V. brasiliensis* Choisy are typical Cerrado species. By contrast, *Protium* spp. are characteristic of the Amazon Forest, while *C. canjerana* (Vell.) Mart. is a species of second-growth forest. *Psychotria nuda* (Cham. and Schltdl.) Wawra, *K. albopunctata* Saddi., *C. scabra* Pers., *Guatteria villosissima* A. St.-Hil., *Lamanonia ternata* Vell., *Ocotea elegans* Mez., *Tibouchina granulose* (Desr.) Cogn., *S. rugosum* Mart., and *Miconia cinnamomifolia* (DC.) Naudin are all typical of the Atlantic Rain Forest. This group provided 40% of the CPOM attributed to the 20 key species, whereas the Cerrado and Amazon species contributed 22% and 17%, respectively, and second *C. canjerana* provided 5%.

## 4. Discussion

### 4.1. Organic matter dynamics

Leaves were the most important category of allochthonous CPOM collected in the Garcia Stream, contributing 70% of the total CPOM. A similar proportion was recorded by Gonçalves et al. (2006a) for a second-order highland stream in the Brazilian Cerrado, while a slightly smaller value (>50%) was recorded by Zhou et al. (2007) in China. As in the present study, twigs were the second most important category at both these sites, followed by other plant parts. The branches constituted the second-largest component of the terrestrial input in the rainy season, which may reflect the influence of the heavy rains during this period. Similarly in Africa, Magana (2001) also suggested a relationship between heavy rains and an increased input of twigs and other plant parts (60%). While it is an important structural component of fluvial habitats, an increase in this component of the OM, which is more refractory, may represent reduction in available energy resources for aquatic organisms, given its low food quality (Diez et al., 2002; Elosegi et al., 2007).

The highest input of CPOM (leaves) was recorded in October (Fig. 2), which is typically the end of the dry and the beginning of the rainy season. In tropical forests, leaf fall occurs throughout the year, but tends to increase during the dry season (Golley, 1983; Meguro et al., 1979). Drought appears to stimulate leaf fall and CPOM input into tropical streams (França et al., 2009). Some species such as *M. cinnamomifolia* (DC.) Naudin, *V. brasiliensis* Choisy, *C. canjerana* (Vell.) Mart., *G. virbunoides* Cham. & Schltdl., and *C. decandra* Jacq. contributed significantly to the different inputs. These species are deciduous and lose their leaves during the austral autumn and winter (April–October), resulting in an increase in CPOM during this period. Delong and Brusven (1994) recorded a similar pattern, with increased input between August and November (boreal autumn) in a temperate region.

The results of the present study indicate significant seasonal variation in the input and stocks of CPOM in the riparian zone of Garcia Stream, rejecting our hypothesis. This indicates the importance of knowledge of these variations for the understanding of the metabolism and functioning of low-order tropical streams (Maridet et al., 1997). The horizontal input was the largest allochthonous contribution of leaves, and included the largest number of dominant species. This input probably reflects the influence of wind, rainfall, width of the stream, steepness of the banks, and animal movements (Naiman et al., 2005). Although it contributed the smallest amount of CPOM, the vertical input included a wide variety of species, which probably reflects the influence of phenological patterns and seasonal variation in climate (rain and wind, probably the main factors in this study), as well as the diversity of species along the stream. In a study of an Atlantic Rain Forest stream, in contrast, Afonso et al. (2000) found that the vertical input contributed the most CPOM (713 g $m^{-2}$ $year^{-1}$), followed by the horizontal input (421 g $m^{-2}$ $year^{-1}$). This difference from the present results may reflect local factors, such as species composition and phenological patterns.

The benthic stock represents the CPOM progressively accumulated in the stream, the monthly budget inputs, transport, export, and the sum of decomposition rates (Pozo and Elosegi, 2005). The benthic stock is partially influenced by the horizontal and vertical inputs, as a contribution to the nutrient content of the stream.

França et al. (2009) and Gonçalves et al. (2006a) also found that the CPOM present in the benthic stock was greater than the sum of the different inputs, which indicates low rates of decomposition of this allochthonous material (and may also be related to transport from upstream), as observed by Gonçalves et al. (2006b, 2007) in a headwater stream of the Cerrado.

In comparison with the results of the present study, Magana (2001) and França et al. (2009) recorded much higher benthic stock and input values. By contrast, Henry et al. (1994) found a mean horizontal input similar to that recorded here. Afonso et al. (2000) recorded a vertical input of only 7 g $m^{-2}$ $month^{-1}$ in an open area, and 59 g $m^{-2}$ $month^{-1}$ in an area of closed-canopy vegetation, with a horizontal input of 10 g $m^{-2}$ $month^{-1}$ and 35 g $m^{-2}$ $month^{-1}$, respectively, in the two areas. The sampling procedures in the present study were similar to those used by Gonçalves et al. (2006a,b) and França et al. (2009). The other studies were based on samples of different sizes and composition, but even so, comparison of their results indicates that variation in the production of CPOM is related to factors such as the characteristics of the riparian vegetation (Rodrigues and Leitão-Filho, 2001) and the physical environment (Vannote et al., 1980; Hutchens and Wallace, 2002), and the degree of anthropogenic fragmentation (Fahrig, 2003).

### 4.2. The Riparian community

The taxonomic diversity of the plant community surveyed here emphasizes its complexity and the immense variety of ecological relationships that exist in tropical ecosystems (Laurance and Bierregaard, 1997). The substantial contribution to the CPOM of some species, such as *Protium* spp., *C. canjerana* (Vell.) Mart., *C. scabra* Pers., and *C. decandra* Jacq., indicates that they are key species in the energy and nutrient dynamics of the study stream. However, the data also indicate that some species that contributed much less CPOM overall, e.g., *Roupala brasiliensis* (Klotzsch) K.S.Edwards and *Tibouchina granulosa* (Desr.) Cogn. can also be considered important species. The importance of these species is reinforced by the close links between the aquatic and terrestrial ecosystems, which influence energy flow and nutrient cycling within the riparian zone (Hutchens and Wallace, 2002; Naiman et al., 2005).

In the Rio Doce basin, França et al. (2009) identified 44 species, less than one-third of the number recorded in the present study. This difference may reflect the variation between sites, such as the biome, dominant vegetation type, and altitude. Whatever the determinants, the considerable diversity of plant species found in some of these tropical systems is an additional factor complicating the study of their dynamics. Available studies of tropical headwater streams indicate a close connection between terrestrial and aquatic ecosystems through their riparian zones (Srivastava and Vellend, 2005; Vondracek et al., 2005; Becker et al., 2007). All these aspects need to be taken into account in the development of conservation strategies, management programs, and environmental legislation.

A survey of the riparian vegetation of headwater streams in the Brazilian Cerrado (Méio et al., 2003) indicated that between 8% and 19% of the plant species were Amazonian in origin, and a further 30–40% were typical of the Atlantic Rain Forest, a pattern confirmed in the present study. These proportions may vary according to the geographic distribution of the different species and local variations in phyto-physiognomy (Oliveira-Filho and Ratter, 1995). In addition, riparian vegetation is clearly very important as an ecological corridor for the dispersal of plant and animal species between different phyto-physiognomic formations (Méio et al., 2003). Some of the species recorded here are common in Brazilian riparian habitats. While the Atlantic Rain Forest has a different species composition from the present study (Afonso et al., 2000), some species or genera (e.g., *Croton*, *Cabralea*, *Vernonia*, *Alchornea*, *Casearia*, *Machaerium*, and *Ocotea*) are common in both types of vegetation. At a second Cerrado site, França et al. (2009) recorded a very similar species composition (*Casearia* sp., *Ocotea* sp., *Pera glabrata*, and *Tapirira guianensis*) to that observed here, with several plant genera in common. Information of this type is essential for efficient mapping of species dispersal along tropical riparian corridors, and for the development of effective conservation strategies for these riparian zones. This vegetation can be especially vulnerable to impacts resulting from the expansion of agricultural frontiers (Fahrig, 2003; Vondracek et al., 2005; Vandermeer and Perfecto, 2007), including the introduction of exotic species (Cushman and Gaffney, 2010). The data presented here will be useful for the development of guidelines for the restoration or regeneration of the vegetation adjacent to tropical rivers, as suggested by Strayer and Findlay (2010).

In contrast to the studies of Gonçalves et al. (2006a) and França et al. (2009), who found that a large proportion of the input of OM (70% of the CPOM) was contributed by less than 30% of the species, the present study indicated that 40% of the CPOM was provided by only 16% of the species (as shown by the analysis of indicator species). This innovative analysis takes into consideration not only the total CPOM, but also the relative frequency of the contribution of each species during the course of the year, in particular those that lose their leaves during periods (e.g., the rainy season) when the input of other species is reduced. This suggests an alternating pattern of the relative importance of different species over the course of the year, with some being key species in the dynamics of CPOM in low-order streams, based on their seasonal contribution to the input of CPOM.

The CPOM dynamics of Garcia Stream showed a highly seasonal pattern due to the influence of precipitation levels, which leads us to reject our hypothesis, that no significant seasonal variation would be observed, based on the relative stability of climatic conditions, and the high productivity that is typical of tropical systems. Leaves were the principal source of allochthonous CPOM in the riparian zone. The different types of input varied according to intrinsic factors. A number of species characteristic of the Amazon and Atlantic Rain forests were identified, together with species of the Cerrado, indicating that the riparian vegetation should not be considered part of a single forest domain, but rather a unique and integrated system that functions as an ecological corridor for species dispersal. The data obtained here confirmed the ecological complexity of the system, derived from the diversity of plant species and the seasonal dynamics of CPOM, related to the phenology of the plant community. The species *Protium* sp. 2, *Cassia ferruginea*, *C. canjerana*, *C. decandra*, *C. scabra*, *R. brasiliensis*, *T. granulosa*, and *Nectandra megapotamica* played an important role in the dynamics of the CPOM of the riparian zone, due to their consistent and high contribution to the system's CPOM. It seems likely that this pattern is related to the high species diversity in the riparian zone, given that almost 200 plant species were recorded in a half-hectare plot, with the potential for considerable variation in the abundance and productivity of each species.

We emphasize the need for evaluation of the potentially important species in the energy flow and nutrient cycling of tropical ecosystems. Future studies should concentrate on understanding the importance of each plant species to the functioning of the riparian zone, in particular species that contribute small quantities of allochthonous CPOM overall, but are relatively important during periods of low input, as observed in the present study. Ultimately, nutrient intake can be a rough measure of energy input, and a reduction in energy input will affect growth and reproduction. The results of this study may contribute to the development of management programs and conservation strategies for the riparian zone, in particular the selection of key species for reforestation projects.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.aquabot.2013.03.005.

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