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Landcover changes and δ^{13}C composition of riverine particulate organic matter in the Piracicaba River Basin (southeast region of Brazil)

Abstract—Assuming the paradigm that catchment vegetation is the main source of particulate organic matter (POM) to rivers, the main objective of this study was to determine what the proportion of original C3 carbon from the forest had already been replaced by C4 carbon from sugar cane and pasture in the rivers of the Piracicaba Basin. In order to achieve this objective, we first produced a detailed landcover map using Landsat5-TM images, and then we measured the carbon stable isotopic composition of the particulate riverine organic matter (δ^{13}C-POM) in seven sites along the major rivers and in two sites along a small creek. Sugar cane and pasture (C4 plants) covered almost 60% of the basin area, while silviculture, mostly of other crops, citrus, and forest that are C3 plants, covered 35%. Isotopic studies conducted in large pristine tropical rivers of South America and of Africa have shown that catchment vegetation is the main source of carbon in suspended POM. Our study demonstrates that relatively recent changes (70–80 yr ago) in landcover in the Piracicaba River Basin have already affected the composition of the riverine POM. Therefore, as in natural ecosystems, the vegetation (allochthonous source) plays an important role in the composition of the riverine POM in agricultural systems such as the Piracicaba River Basin. This control can be supported by the good correlation between cumulative area of the basin covered with C4 plants and the δ^{13}C of the riverine POM. However, our study, differently from others, also shows that, during the low water period, in situ processes, such as primary production, may be an important source of carbon to the riverine POM.

Suspended particulate material is important in river systems for several reasons: a large amount of carbon is transported in particulate form (Meybeck 1982), particulate organic matter (POM) provides food for numerous organisms (Naiman 1983), and links upstream to downstream reaches (Cushing et al. 1993). POM also influences heavy metal availability (Sung 1995) and integrates natural and anthropogenic processes in the catchment (Hedges et al. 1994). The stable carbon isotopic composition (δ^{13}C) of the riverine particulate material (POM) has been used to identify the origin of the carbon attached to this fraction (Hedges et al. 1986*a*; Cai et al. 1988; Mariotti et al. 1991; Quay et al. 1992; Bird et al. 1994, 1998; France-Lanord and Derry 1994). These studies have compared the stable carbon isotopic composition of riverine particulate organic matter (δ^{13}C-POM) with those vegetation and soils in their catchment. Such comparisons are particularly effective in situations where the basin landcover is composed of a mixture of C3 and C4 plants. In tropical conditions, the δ^{13}C values of C3 plants range from −34 to −27‰, while the range of δ^{13}C values of C4 plants is much narrower, varying from −14 to −11‰. This large isotopic difference allows the recognition of the relative contribution of each type of vegetation to riverine organic matter.

Isotopic studies conducted in large pristine tropical rivers of South America (Hedges et al. 1986*a*; Cai et al. 1988; Quay et al. 1992) and of Africa (Mariotti et al. 1991; Bird et al. 1994, 1998) have shown that catchment vegetation is the main source of carbon in suspended POM. It also has been demonstrated that vegetation is not the only control; soil and the position of each type of vegetation in the landscape are also important (Mariotti et al. 1991). Furthermore, Hedges et al. (1986*b*) have demonstrated, with the use of radiocarbon dating, that the coarse (>63 μm) and the fine fractions (<63 μm) of the Amazon River have distinct residence times in the basin, supporting an early hypothesis that the fine fraction had its origin in the soil, whereas the coarse fraction is derived directly from vegetation.

Rivers draining forested watersheds in the tropics have δ^{13}C-POM typical of this type of vegetation, with values ranging approximately from −30 to −27‰ (Table 1). Rivers draining savannas (with C4 plants) and mixed savanna/forest regions showed a large range of the δ^{13}C-POM, varying from −28 to −19‰ (Table 1). Although covered mainly by C4 savannas, a sub-basin of the Congo River had δ^{13}C-POM values typical of C3 vegetation, while the Mbam River, a tributary of the Sanaga River in Cameroon, had a δ^{13}C-POM near −19‰ in its fine fraction, indicating the presence of C4 material (Table 1). The first example indicates, as previously mentioned, that not only is the vegetation of the basin an important control of the δ^{13}C-POM but also of its spatial distribution in the landscape (Mariotti et al. 1991).

These studies have been conducted on relatively pristine and large tropical rivers, where C4 or C3 vegetation are well established in the catchment; the POM probably had enough time to acquire the isotopic signal of the catchment vegetation. Less is known about the origin of particulate organic carbon in smaller catchments, where the original forest vegetation has been recently (70–80 yr ago) replaced by C4 plants, such as sugar cane or tropical grasses. Studies in such areas are important because it is possible to determine to what extent landcover /use changes have altered the δ^{13}C-POM and provide information on the rates of organic carbon transfer from the catchment to the river that is difficult to obtain in relatively unaltered drainage basins.

The Piracicaba River Basin is a mesoscale catchment ($\approx 10^4$ km^2) in the southeast region of Brazil, where a change from C3 to C4 vegetation has recently occurred. Less than 10% of the original vegetation is left and a significant area (56%) is now covered with C4 plants. The agricultural C4 material is incorporated into the soil. A soil survey made in the Piracicaba River Basin has shown that after 12 and 50 yr of sugar-cane cultivation, the δ^{13}C of the surface soil organic matter changed from its original −25.1‰ to −23.0‰ and −20.2‰, respectively. These figures indicate that after 50 yr, approximately 40% of the forest (C3) carbon was replaced by sugar-cane (C4) carbon (Vitorello et al. 1989).

Table 1. δ^{13}C values (‰) of suspended particulate organic carbon within different rivers.

River	Fine	Coarse	Vegetation	Reference
Jaguari	−25.8	−25.8	Agricultural C3/C4	This study
Atibaia	−26.7	−25.9	Agricultural C3/C4	This study
Piracicaba	−25.5	−24.6	Agricultural C3/C4	This study
Piracicamirim	−20.5	−25.6	Agricultural C4	This study
Amazon	−26.8	−27.8	Forest	Quay et al. 1992
Madeira	−26.8	−27.4	Mostly forest	Quay et al. 1992
Içа	−28.3	−28.6	Forest	Quay et al. 1992
Japurá	−28.2	−28.8	Forest	Quay et al. 1992
Juruá	−28.9	−29.3	Forest	Quay et al. 1992
Purus	−28.8	−29.9	Forest	Quay et al. 1992
Negro	−28.2	—	Forest	Quay et al. 1992
Jutaí	−30.1	−29.1	Forest	Quay et al. 1992
Araguaia	−28.1	−27.7	Forest/Cerrado	Bird et al. 1992
Tocantins	−29.3	−27.0	Forest/Cerrado	Bird et al. 1992
Mbam	−18.8	−20.5	Savanna	Bird et al. 1992
Sanaga	−21.3	−24.2	Savanna	Bird et al. 1992
Sanaga	−29.0	−29.2	Forest	Bird et al. 1992
Congo	−26.7*	—	Savanna/Forest	Mariotti et al. 1991
Niari	−21.2*	—	Savanna/Forest	Mariotti et al. 1991
Djoue	−26.9*	—	Savanna	Mariotti et al. 1991
Djili	−27.6*	—	Savanna	Mariotti et al. 1991
Loua	−28.3*	—	Savanna	Mariotti et al. 1991

* Suspended solids samples were not divided into fine and coarse fractions.

Assuming the paradigm that catchment vegetation is the main source of POM to rivers, what is the proportion of the original C3 carbon from the forest already replaced by C4 carbon from sugar cane and pasture in the rivers of the Piracicaba Basin? To answer this question we first produced a detailed map of the vegetation in this basin using Landsat Thematic Mapper (TM5) images, and we measured the δ^{13}C of the coarse (>63 μm) and fine (<63 μm) POM fractions at different sites within the basin. Additionally, we measured the δ^{13}C-POM of the fine and coarse fractions of Piracicamirim Creek, which drains a small-scale catchment (10^1 km^2) that has been almost entirely converted to C4 plants (sugar cane).

The Piracicaba River basin (12,400 km^2) is located in the southeast region of Brazil within the state of São Paulo (Fig. 1). The basin had almost three million inhabitants in 1993, 92% in urban centers and 8% in rural areas (São Paulo 1994). It has three main sub-basins: the Jaguari (3,400 km^2), Atibaia (3,000 km^2), and the Piracicaba (6,000 km^2); the latter being formed by the junction of the previous two. These rivers flow from east to west in a stretch approximately 250 km long. The average discharges of the Jaguari and Atibaia rivers near their confluence are 55 and 37 m^{-3} s^{-1}, respectively. The average discharge of the Piracicaba River at the outflow of the basin is 156 m^3 s^{-1}. The Piracicamirim is a small river (23 km^2) located in the west side of the Piracicaba River Basin (Fig. 1). Its annual average discharge is equal approximately to 3 m^3 s^{-1}.

The land-use/landcover map of the Piracicaba River Basin was generated with the digital supervised classification of two TM/Landsat5 images (path-row: 220-76 and 219-76), using the maximum likelihood method (Jensen 1996). The scenes of the study area (of 24 July and 13 June 1993) were acquired from the National Institute of Spatial Research (INPE), in São Paulo, Brazil. Bands 1, 2, 3, 4, 5, and 7 were digitally processed to produce a land-use/landcover map with the following categories: water, urban areas, sugar cane, citrus, annual crops, silviculture, and forest.

The digital processing of images included the following steps: (1) Geometric correction: at least 80 control points for each scene were derived from hydrographic and topographic maps Brazilian Institute for Geography and Statistics (IBGE), 1 : 50.00) and employed in the geometric correction. The root mean square was 1.8 pixels. For the final correction of the images we used a first-order polynomial, with nearest-neighbor resampling (final spatial resolution 30 × 30 m). All scenes were then projected in a common system, Universal Transverse Mercartor, Datum Corrego Alegre, Spheroid Southamerican 1969; (2) radiometric rectification: performed using the radiometric rectification method as describe in Hall et al. (1991); and (3) digital classification: training sites for the supervised classification were acquired using field observations and aerial photographies. Each sample had at least 700 pixels per class (100 × number of classes; Jensen 1996). The classification accuracy was checked through a field survey. We visited 100 randomly selected points, and 80% of them had corresponding land use.

After the initial classification, the landcover classes were grouped in three categories: C4 plants (sugar cane, pasture, and corn), C3 plants (silviculture and other C3 crops), and other uses that include cities and areas covered with water. All image processing and analysis was carried out using Geographic Information Systems (GIS) Arc-Info. The cumulative area of a river sampling site covered with C4 plants represents the upstream watershed area from that sampling site covered with C4 plants.

A total of 20 water samples was collected in each of two sites along the Piracicaba, three sites along the Atibaia, and

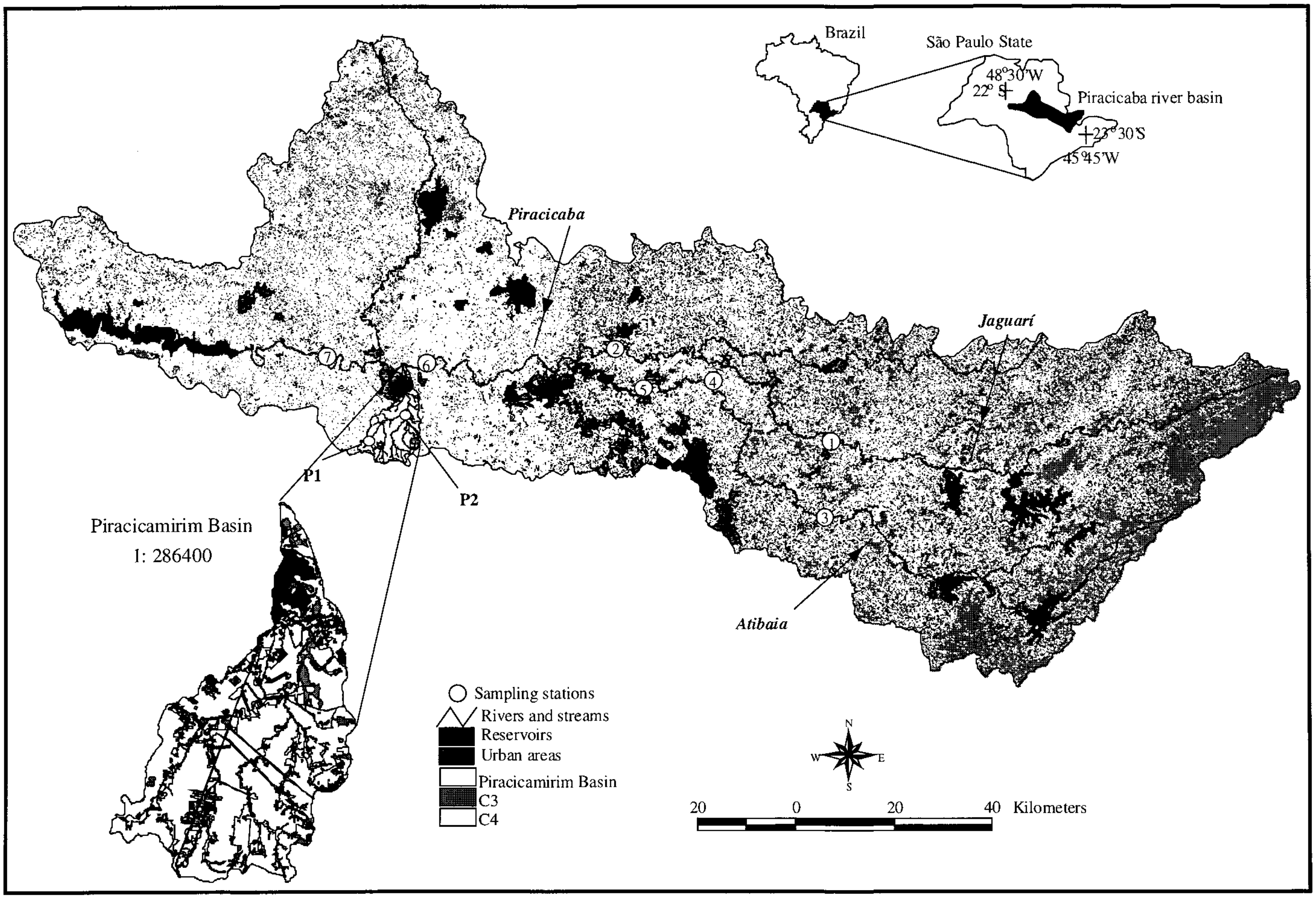

Fig. 1. Landcover of the Piracicaba River Basin in 1993 and sampling sites. Jaguari River—sampling sites 1 and 2; Atibaia River—sampling sites 3, 4, 5; and Piracicaba River—sampling sites 6 and 7. White area covered with C4 plants and gray area covered with C3 plants.

two sites along the Jaguari rivers from January 1996 to May 1997. Because the concentrations of particulate were not always enough for the analysis, some of the averages do not include all 20 sampling days. In Piracicamirim Creek, a total of 17 water samples were collected at two sites, from February 1997 to July 1998. The high and low water periods spanned October to March and April to September, respectively. Sampling sites 1 and 2 were located along the Jaguari River, sites 3, 4, and 5 along the Atibaia River, and sites 6 and 7 along the Piracicaba River. Sites along the Piracicamirim Creek were named P1 and P2 (Fig. 1).

At each site 100–200 liters of water were collected from the river surface in the middle of the channel using a pump. The water from the river was sieved (>63 μm) in order to separate the coarse fraction of the particulate suspended material. The sieved fraction was stored in plastic containers and transported to the laboratory. In the laboratory, tangential ultrafilter equipment (Amicon DC10) was used to separate the fine particulate fraction (<63 μm and >0.1 μm). After filtration, the material retained was dried to constant weight in an oven at 60°C.

Dried samples were combusted for 12 h with CuO in evac-

Table 2. Average δ^{13}C values (‰) for high and low water period.

River	High water	Low water
Jaguari River		
Fine fraction*	−24.8	−27.0
Coarse fraction*	−25.3	−26.1
Atibaia River		
Fine fraction*	−25.8	−27.9
Coarse fraction*	−25.8	−26.2
Piracicaba River		
Fine fraction (NS)†	−24.7	−24.4
Coarse fraction (NS)	−25.4	−25.8
Piracicamirim Creek		
Fine fraction*	−21.4	−19.0
Coarse fraction*	−26.0	−25.0

* Asterisk indicates statistically significant result.
† NS, not significant.

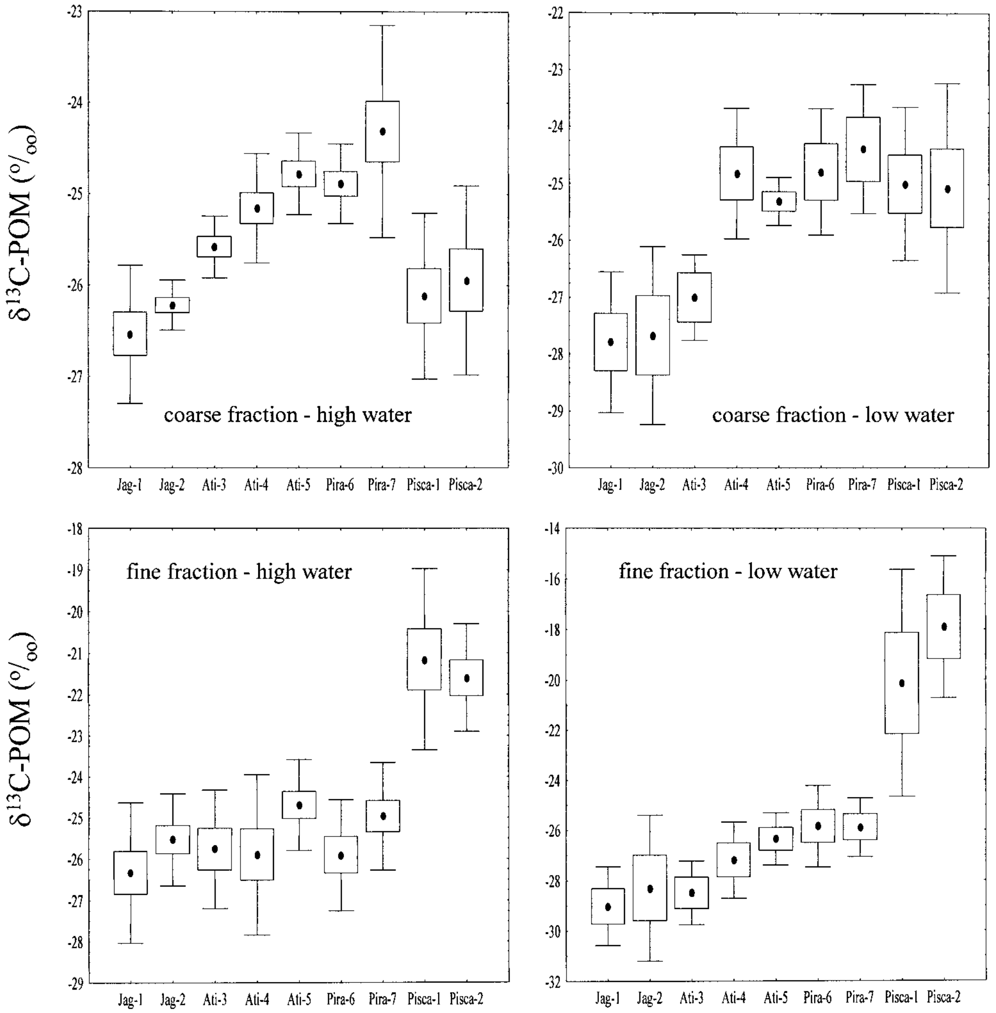

Fig. 2. Spatial variability of δ^{13}C-POM values in the Piracicaba River Basin. Dot inside the box is the average. The box is the standard-error of the average and bars are the standard deviations.

uated tubes at 550°C. Isotope measurements were performed with a Finnigan Delta-E mass spectrometer fitted with dual inlet and dual collector systems. Results are expressed in δ^{13}C relative to Pee Dee Belemnite (PDB) isotopic standard, defined as:

$$\delta^{13}\text{C, ‰} = (R_{\text{sample}}/R_{\text{std}}) - 1 \times 1{,}000,$$

where R_{sample} and R_{std} are the ^{13}C : ^{12}C of the sample and standard, respectively. Samples were analyzed at least in duplicate with a maximum difference of 0.2‰ between replicates.

The average values are presented with ±1 standard deviation and by the number of samples (n) used to compose that average. To test for differences among populations, we used the Tukey honest significant difference for unequal N test through the STATISTICA package.

Landcover of the Piracicaba River Basin in 1993 was dominated by sugar cane that covered 35% of the basin area, followed by pasture (24%), silviculture (16%), other crops (9%), citrus (6%), cities (4%), forest (3.5%), and water (2%). Sugar cane and pasture are C4 plants, while silviculture, most of the other crops, citrus, and forest are C3 plants. Regrouping the landcover types into C4 and C3 categories, C4 occupied 59% of the basin area and C3 approximately 35% (Fig. 1). In the Piracicamirim sub-basin, the percentage of the area covered by sugar cane (40%) is higher than in the Piracicaba Basin. Pasture covered the second largest area (19%), followed by cities (15%), crops (9.5%), silviculture (7.5%), forest (5.5%), and citrus (2%), resulting in 60% of the landcover with C4 and 25% with C3 plants, respectively.

There was large variability in the δ^{13}C of both fine and coarse POM fractions in river waters of the Piracicaba Basin. In the three sites of the Atibaia river, δ^{13}C-POM of the fine fraction ranged from −31.1 to −22.7‰, with an average of −26.7 ± 1.37‰ ($n = 43$). The δ^{13}C of coarse POM also had large variability, ranging from −29.6 to −23.2‰, with an average (−25.9 ± 1.23‰, $n = 47$), statistically heavier than the fine fraction ($P < 0.01$). Variability in the Jaguari River (two sites) was similar to the Atibaia, with an average δ^{13}C that was not statistically different from the Atibaia. The δ^{13}C-POM of the fine fraction ranged from −31.9 to −23‰, and averaged −25.8 ± 1.89‰ ($n = 32$). The coarse fraction ranged from −29.0 to −24.0‰, with an average similar to

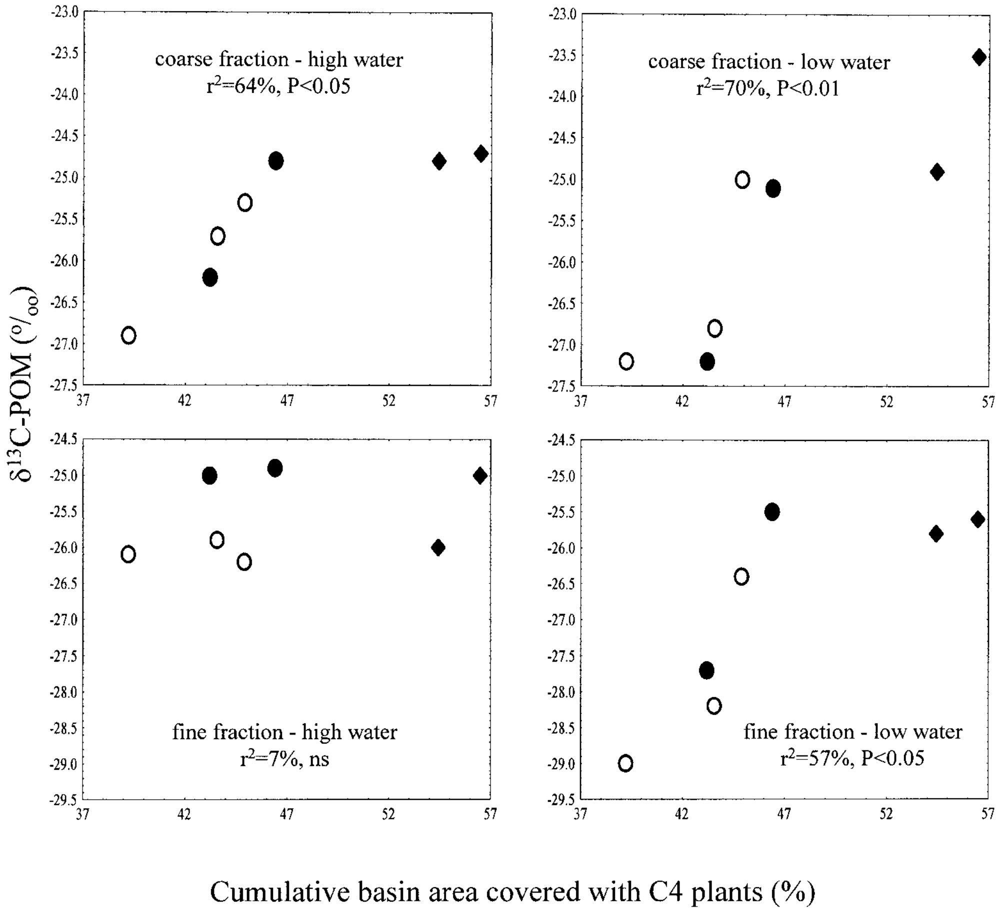

Fig. 3. Seasonal average δ^{13}C-POM values as a function of the cumulative area of the Piracicaba Basin covered with C4 plants. Open circle—Atibaia River, closed circle—Jaguari River, and closed diamond—Piracicaba River.

the fine fraction (−25.8 ± 1.21‰, $n = 31$). The variability of the δ^{13}C-POM values in the Piracicaba River was smaller than observed in its two tributaries. The fine fraction varied from −28.1 to −23.1‰, with an average (−25.5 ± 1.37‰, $n = 32$) that was statistically heavier than the Atibaia ($P < 0.01$) but not different from the Jaguari River. The corresponding variability of the coarse fraction collected in two sites along the Piracicaba ranged from −26.1 to −20.8‰. The average δ^{13}C was −24.6 ± 0.96‰ ($n = 31$), which is statistically heavier than the corresponding fine fraction average and statistically different from the averages of the coarse fractions of the Atibaia and Jaguari rivers ($P < 0.01$).

Seasonal differences were observed in the fine fraction of the Atibaia and Jaguari ($P < 0.01$), where the δ^{13}C-POM values were lighter at the low water than at high water (Table 2). Except for the δ^{13}C values of the fine fraction during the high water period, the δ^{13}C values were always heavier downstream. This downstream isotopic enrichment was especially large in the Jaguari and Atibaia rivers in comparison with the Piracicaba River (Fig. 2).

The δ^{13}C-POM of the fine fraction of the Piracicamirim Creek ranged from −26.5 to −13.8‰, with an average of −20.5 ± 2.81‰ ($n = 28$). The overall average δ^{13}C of the coarse fraction was significantly lighter (−25.6 ± 1.32‰, $n = 32$) and ranged from −27.9 to −22.2‰. The δ^{13}C average values for both fractions were heavier during the low water period ($P < 0.01$), trending in the opposite direction from the larger rivers of the Piracicaba Basin (Table 2). There was no downstream difference in the δ^{13}C values of either POM fractions from Piracicamirim Creek.

The major control of the δ^{13}C-POM appears to be the vegetation of the catchment (Hedges et al. 1986*a*; Quay et al. 1992; Bird et al. 1994, 1998), although soil texture may also exert some influence (Mariotti et al. 1991). In catchments where sandy soils predominate, it appears that δ^{13}C-POM is more influenced by the riparian vegetation. Where there is a predominance of more impermeable clay-rich soils, surface runoff becomes more important and the entire vegetative cover of the basin becomes important (Mariotti et al. 1991). In the Piracicaba River Basin, most of the soils have medium to high clay texture. From 268 B-horizons analyzed, 54% had clay to very clay texture, 38% medium texture, and only 8% had sand texture (C. E. Cerri unpubl. data). Therefore, based on the predominance of clay soils in the basin, it would be expected that δ^{13}C-POM values should reflect the isotopic composition of the predominant vegetation in the basin. In fact, within the Piracicamirim sub-basin, where C4 plants cover more than 60% of the area, the δ^{13}C-POM of

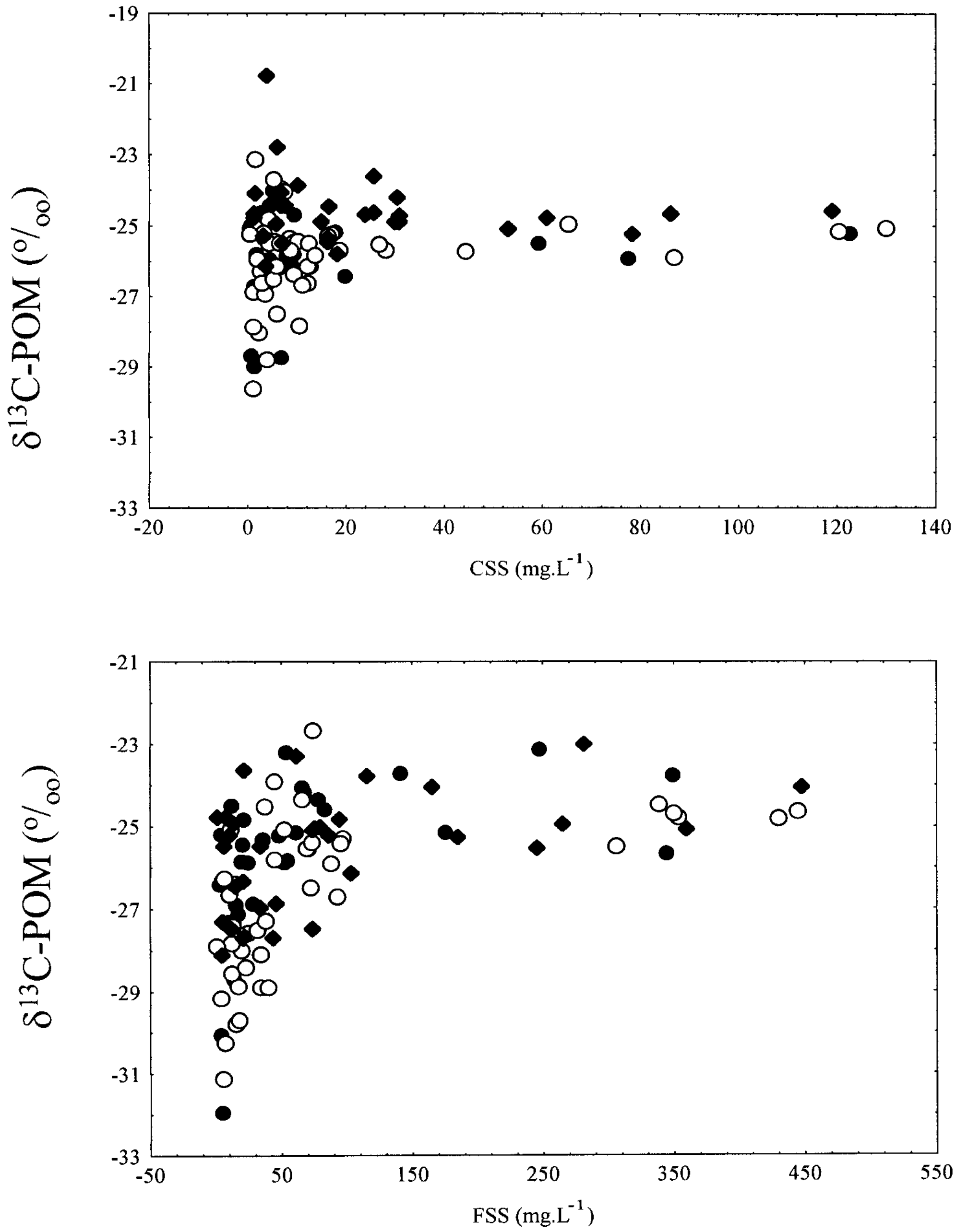

Fig. 4. δ^{13}C-POM against coarse (CSS) and fine suspended sediments (FSS). Sediment data were obtained from Martinelli et al. (1999). Open circle—Atibaia River, closed circle—Jaguari River, and closed diamond—Piracicaba River.

the fine fraction does have the heaviest measured values (Table 1). In addition, there was a reasonable correlation between the seasonal average δ^{13}C-POM and the cumulative area covered with C4 plants among sampling sites along the larger rivers of the Piracicaba Basin (Fig. 3).

The only exception to this correlation was for POM fine fractions during the high water period. At this time, the δ^{13}C-POM of the fine POM was heavier throughout the basin, independent of the size of the area covered with C4 plants, indicating a strong influence of C4 vegetation (Fig. 2). The absence of correlation for the high water period is probably due to high surface runoff (more than 70% of the total annual rainfall occurs during this period), which carries fine particles from sugar-cane and pasture C4 fields to the rivers. Supporting this hypothesis is the fact that heavier δ^{13}C-POM values of the fine fraction were associated with high sediment load occurring during high water periods (Fig. 4). The same type of correlation was found in the Sanaga River (Cameroon) that drains extensive natural savanna fields (Bird et al. 1998). During the dry season the δ^{13}C-POM of the Sanaga River became lighter due to the presence of a riparian forest (C3 vegetation) (Bird et al. 1998). However, because there is no gallery forest left on the banks of the larger rivers of the Piracicaba Basin, the isotopically light source could not be the same as for the Sanaga River. The most likely isotopically depleted source is in situ primary production. During the low water, conditions are favorable for phytoplankton growth. Light penetration is improved during low water because river turbidity has decreased. The total sediment concentration in sampling site 6 decreased from an average of approximately 300 mg liter^{-1} during the high water period to less than 50 mg liter^{-1} during the dry, low water season (Martinelli et al. 1999). In addition, concentrations of nutrients, mainly nitrogen forms, were higher during the low water period (Martinelli et al. 1999). We did not directly measure phytoplankton growth, but the number of organisms per water volume was measured by Faustino (1998), who found the highest values in the rivers of the basin near the end of the dry season. Other indirect evidence was the color of the river water at the upstream regions, which became greenish during the low water period (e.g., 1 August 1996). On that day the δ^{13}C-POM of the fine and coarse fractions collected in sampling site 1 were -32 and -29‰, respectively. On the same day at sampling site 3, the δ^{13}C of both POM fractions were -30 and -31‰, respectively. These values are similar to the average δ^{13}C values of four pure filamentous phytoplankton samples collected in the basin (-31.0 ± 4.7‰), suggesting that in situ primary production could be an important source of light carbon to the river POM during the dry season. It is also likely that phytoplankton produced in a large eutrophic reservoir, just upstream from the beginning of the Piracicaba River (Fig. 1), was responsible for the unexpectedly light δ^{13}C-POM of the Piracicaba River (Fig. 3). Part of the isotopically heavy particulate material provided by the Atibaia River to the reservoir is probably being trapped within the reservoir and replaced by isotopically depleted material produced by phytoplankton. A few kilometers down the reservoir, this material mixes with POM from the Jaguari River when forming the Piracicaba River. A similar trend was observed in the Sanaga River, where the isotopically enriched POM from natural savannas was replaced by isotopically depleted material produced by phytoplankton (Bird et al. 1998).

The major difference between the δ^{13}C-POM of the fine and coarse fractions was observed in the Piracicamirim Creek (Table 2). While the difference between the fine and coarse fractions in larger rivers of the basin was approximately 0.5‰ during the high water and 1.5‰ during the low water, in the Piracicamirim Creek this difference was 4.6‰ during the high water and 6.0‰ during the low water (Table 2). The upstream reaches of the Piracicamirim still have a fragmented riparian forest in its banks. In these upstream regions the creek is only 1–2 m wide and, consequently, the riparian forest shaded the entire creek sector. This forest could be a source of isotopically depleted coarse detritus to the creek. The average δ^{13}C of leaves from four common species of trees in these areas was -31.0 ± 2.1‰ and the average for wood was equal to -30.1 ± 2.0‰ (M. Bernardes unpubl. data). Isotopically enriched fine particles from the predominant vegetation in the basin (sugar cane) is likely to be the source of the riverine fine fraction.

Our study demonstrates that relatively recent changes (70–80 yr ago) in landcover have already affected the composition of the riverine POM. Therefore, as in natural ecosystems, the vegetation (allochthonous source) plays an important role in the composition of the riverine POM in agricultural systems such as the Piracicaba River Basin. However, our study also shows that in situ processes, such as primary production, may be an important autochthonous additional source of carbon to the riverine POM during the low water period. Consequently, the relationship between cumulative basin area covered with C4 plants and δ^{13}C-POM during the low water (Fig. 3) may not be due exclusively to changes in the proportion of the allochthonous C3 and C4 sources but also to spatial changes in the proportion of autochthonous (phytoplankton) and allochtonous (C4 and C3 plants) carbon sources. The upstream sites would have a mixture of phytoplankton and C3 plant material, while in the downstream sites the presence of C4 material in the particulate would increase (Fig. 3).

Finally, the observed large spatial and temporal variability in the carbon isotope composition indicates that different types of POM are entering the Piracicaba River Basin at different times. Any attempt to understand the dynamics of riverine organic matter in mesoscale basins ($\approx 10^4$ km^2) must take this high variability into account. GIS-based assessments of vegetation distributions and dynamics should prove a powerful tool for interpreting river POM compositions in relation to drainage basin characteristics.

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Plankton availability and retention efficiencies of cold-seep symbiotic mussels

Abstract—Mussels from deep-sea methane/sulfide seeps in the Gulf of Mexico supplement their symbiotically acquired nitrogen by feeding selectively on nitrogen-rich bacterioplankton. The previously unknown natural diet of the mussels consists of bacteria, *Synechococcus*-type cyanobacteria, and protozoans. Overall retention increased with increasing mussel size, though the largest mussels did not retain bacteria. Mussels can obtain as much as 0.12 μmol N g^{-1} h^{-1} by filter feeding on natural water-column communities. Previous calculations indicate that nitrogen acquired through the symbionts is inadequate for maximal growth, but our conservative estimates suggest that nitrogen obtained by filter feeding is similar to that acquired by symbionts and may be an important component in the nutritional requirements of seep mussels. Additionally, we conducted a series of in situ measurements of flow and food availability over an extensive mussel bed located at the Brine Pool. Our measurements indicate that biogenic flow due to mussel pumping generates near-bottom turbulence that prevents the development of a food-depleted layer over the mussel bed.

Deep-sea hydrothermal vents and methane/sulfide cold seeps support a variety of benthic animals that obtain most or all of their nutritional needs from endosymbiotic chemosynthetic bacteria (Corliss et al. 1979; Paull et al. 1984; Kennicutt et al. 1985; Kulm et al. 1986; Brooks et al. 1987; MacDonald et al. 1990*b*). The nutritional requirements and energy budgets of some wholly chemoautotrophic forms have been well characterized (Fisher 1990; Childress and Fisher 1992), but the nutritional role of heterotrophy in mixotrophic species is poorly understood. Various clams and mussels are among the most common organisms inhabiting vents and seeps (Paull et al. 1984; MacDonald et al. 1990*a,b*). Carbon isotope ratios, δ^{13}C, for these bivalves are often similar to values for methane (Rau 1981; Kulm et al. 1986; Brooks et al. 1987; Kennicutt et al. 1992; Fisher et al. 1994), indicating that carbon for growth is obtained via translocation from the symbionts. Nitrogen isotope ratios, δ^{15}N, are much more variable, indicating a broad range of nitrogen sources. Very negative values in some populations are indicative of symbiotically assimilated dissolved inorganic nitrogen (DIN), whereas positive values in other populations suggests that at least some of the nitrogen is obtained heterotrophically (Brooks et al. 1987; Kennicutt et al. 1992; Fisher et al. 1994). However, the feeding ecology of vent and seep bivalves is unknown, probably because available foods in these systems, mostly particles <5 μm, and grazing on them by macroinvertebrates were extraordinarily difficult to study prior to the application of laser-based technologies (Gili and Coma 1998).

The cold seep mussel *Bathymodiolus childressi,* and pre-