Influence of landscape evolution on the distribution of floristic patterns in northern Amazonia revealed by $\delta^{13}C$ data



H. ZANI,¹ D. F. ROSSETTI,^{1*} M. L. C. COHEN,² L. C. R. PESSENDA³ and E. H. CREMON¹

¹Divisão de Sensoriamento Remoto, Instituto Nacional de Pesquisas Espaciais, 12245-970-São José dos Campos, SP, Brazil ²Centro de Geociências, Universidade Federal do Pará, Belém, PA, Brazil ³Laboratório de ¹⁴C, Universidade de São Paulo, SP, Brazil

Received 14 June 2012; Revised 28 September 2012; Accepted 5 October 2012

ABSTRACT: The Amazonian lowlands include large patches of open vegetation which contrast sharply with the rainforest, and the origin of these patches has been debated. This study focuses on a large area of open vegetation in northern Brazil, where $\delta^{13}C$ and, in some instances, C/N analyses of the organic matter preserved in late Quaternary sediments were used to achieve floristic reconstructions over time. The main goal was to determine when the modern open vegetation started to develop in this area. The variability in $\delta^{13}C$ data derived from nine cores ranges from -32.2 to -19.6%, but with nearly 60% of data above -26.5%. The most enriched values were detected only in ecotone and open vegetated areas. The development of open vegetation communities was asynchronous, varying between estimated ages of 6400 and 3000 cal a BP. This suggests that the origin of the studied patches of open vegetation might be linked to sedimentary dynamics of a late Quaternary megafan system. As sedimentation ended, this vegetation type became established over the megafan surface. In addition, the data presented here show that the presence of C₄ plants must be used carefully as a proxy to interpret dry paleoclimatic episodes in Amazonian areas. Copyright © 2012 John Wiley & Sons, Ltd.

KEYWORDS: δ^{13} C isotope; climate; landscape evolution; megafan; open vegetation patches.

Introduction

Areas of open vegetation in Amazonia have received much attention from biogeographers and paleoecologists, as they potentially represent a relict ecosystem related to Late Pleistocene and/or Holocene dry periods (Absy *et al.*, 1991; Servant *et al.*, 1993; Freitas *et al.*, 2001). In some instances, they have also been related to intense lixiviation and podzolic soil formation favored by high precipitation rates (Sioli and Klinge, 1961; Bravard and Righi, 1989). This second most extensive vegetation type in Amazonia is characterized by low biomass (Anderson, 1981) and frequent, sharp contacts with the dense rainforest. The unexpected open vegetation patches within a generally forested area is intriguing, and their origin remains the subject of debate.

Several studies have postulated that Late Pleistocene and Holocene climate changes influenced the modern Amazonian landscape (e.g. Tricart, 1985; Freitas *et al.*, 2001; Latrubesse and Nelson, 2001; Latrubesse, 2002; Anhuf *et al.*, 2006). This hypothesis states that during the dry periods open vegetation communities expanded over forest. In this regard, the modern patches of open vegetation are closely related to paleoclimates. However, there would be many questions regarding whether the Quaternary climate had significant influence on the composition and distribution of modern plants in Amazonia (Irion *et al.*, 1995; Colinvaux *et al.*, 1996; Colinvaux and Oliveira, 2000; Bush *et al.*, 2004; Mayle and Power, 2008).

Sedimentary dynamics due to tectonic reactivations has been proposed as an important control on the development of Amazonian vegetation over time (reviewed by Rossetti *et al.*, 2012a). Areas with alluvial sedimentation under mild tectonic subsidence became sites favorable to the growth of open vegetation, which forms patches in sharp contact with surrounding rainforest. Answering questions concerning when and where these vegetation types evolved is crucial for

*Correspondence: D. F. Rossetti, as above. E-mail: rossetti@dsr.inpe.br discussing the main factors that controlled their establishment in this ecosystem.

Further investigation is needed to better understand the modern vegetation distribution in Amazonian areas. In general, pollen analysis has been the most useful tool for reconstructing vegetation dynamics through time. Where pollen preservation is low, such as in areas with prevalence of sand deposition, δ^{13} C of organic matter has been commonly used for reconstructing vegetation patterns in many other tropical and subtropical areas worldwide (e.g. Victoria et al., 1995; Boutton et al., 1998; Freycon et al., 2010; Sinninghe Damsté et al., 2011). Using this technique, it has been possible to distinguish between plants of C_3 ($\delta^{13}C = -32$ to -20%) and C_4 $(\delta^{13}C = -17 \text{ to } -9.0\%)$ photosynthetic pathways (Boutton, 1996). However, interpretations are not entirely straightforward because the δ^{13} C values of terrestrial C₃ vascular plants overlap those of aquatic vascular plants and phytoplankton from both freshwater and seawater (Wilson et al., 2005a,b). For this reason, δ^{13} C has been combined with C/N to distinguish between terrestrial and aquatic sources of organic matter in sedimentary deposits (Meyers, 1994, 1997; Cloern et al., 2002; Wilson et al., 2005a,b). C/N obtained from total organic carbon (TOC) and total nitrogen (TN) allows the discrimination between freshwater phytoplankton (C/N = 4.0-10.0) and land plants (C/N ≥ 12.0) (e.g. Cloern et al., 2002; Wilson et al., 2005a,b).

 $δ^{13}$ C values from modern soils have been used to infer a middle Holocene expansion of savanna in Amazonia, an event related to a dry climate (Pessenda *et al.*, 2001; Freitas *et al.*, 2001). The work presented here provides $δ^{13}$ C and, to a lesser extent, C/N data from a megafan deposit characterized by areas of open vegetation and tropical forest in northern Brazil. The main aim was to provide a basis for reconstructing plant dynamics through time, and investigate their potential relationship to sedimentary processes during landscape evolution. We provide new data to further discuss the role of climatic fluctuations in the evolution of open vegetation patches interspersed within the Amazonian rainforest.

Study area

The study area, located in the Viruá National Park of northern Amazonia (Fig. 1A), is under a typical tropical climate, with a well-defined dry season and an average annual rainfall of 1800 mm. Average annual temperatures range from 26 to 33 °C (RADAMBRASIL, 1976). The Intertropical Convergence Zone (ITCZ) and the El Niño/La Niña-Southern Oscillation (ENSO) play important roles in determining the interannual rainfall regime in this region (Latrubesse and Nelson, 2001).

Geologically, the Viruá National Park is located in the *Pantanal Setentrional* Basin, an area of Quaternary sediments not yet studied in detail (Santos *et al.*, 1993). This area is bounded to the north, east and west by the Precambrian Guiana Shield. It is also surrounded by alluvial deposits of the Plio-



Figure 1. (A) Location of the studied fan-shaped paleomorphology in the Viruá National Park in northern Amazonia. Note that this region contains several other similar paleomorphologies that are also characterized by open vegetation. (B) A PALSAR image illustrating the Viruá megafan, characterized by its lobate, fan-shaped morphology covered by open vegetation (dark area delineated by the hatched line) in contrast to surrounding rainforest. (C) A drawing of the Viruá megafan extracted from the image shown in B. Note also in this figure the network of mainly SW-flowing distributary channels over the megafan's surface. (D) A topographic profile derived from DEM-SRTM along a longitudinal transect of the megafan (see C for location).

Copyright © 2012 John Wiley & Sons, Ltd.

Pleistocene Içá Formation (Fig. 1A). The Viruá area is dominated by Late Pleistocene to Holocene sands (RADAM-BRASIL, 1976). These deposits display a large fan-shaped morphology related to a megafan (Zani and Rossetti, 2012), and occur with eolian sand dunes and other similar fan-shaped paleomorphologies currently under study (Fig. 1A). A megafan is characterized by extremely low gradients (<0.1°) and a radial, commonly distributary drainage pattern (e.g. Hartley et al., 2010). The Viruá megafan (Fig. 1B, C) displays several characteristics similar to many other megafan analogs described worldwide (e.g. Horton and DeCelles, 2001; Assine, 2005; Nichols and Fisher, 2007; Latrubesse et al., 2012). It is 45 km long and 25 km wide, and displays a drainage network arranged into a distributary pattern (Fig. 1C). In addition, topographic transverse and longitudinal profiles show a convex-up and concave-up shape, respectively (Fig. 1D), produced by sediment aggradation and progradation (Gumbricht et al., 2001, 2005; Chakraborty and Ghosh, 2010; Zani et al., 2012).

A remarkable characteristic of the Viruá megafan is its open vegetation cover, known as *campinarana* (Anderson, 1981; Fig. 2A), in sharp contrast with the surrounding rainforest (Fig. 2B). The open vegetation is mainly Poaceae and Cyperaceae (Gribel *et al.*, 2009), both with a predominant C_4 photosynthetic pathway in many Amazonian areas (e.g. Vidotto *et al.*, 2007). The areas of open vegetation can display forest islands (Fig. 2C, D) dominated by families such as Vochysiaceae and Anacardiaceae (Gribel *et al.*, 2009), all known as typical C_3 plants (Martinelli *et al.*, 1998). Ecotone areas mark the contact between forest and open vegetation, and are characterized by a mixture of C_3 and C_4 plants. The vegetation surrounding the Viruá megafan consists of typical Amazonian rainforests, including the submontane, lowland and alluvial (*várzea*) types (Veloso *et al.*, 1991).

Material and methods

Two separate field trips were undertaken in the dry seasons of 2010 and 2011. The sampling sites were selected by combining, to the extent possible, accessibility and representativeness. Vegetation contrasts were recorded along a transect in the medial section of the megafan mapped by Zani and Rossetti (2012). Due to the absence of outcrops, geological data were derived from nine shallow cores (Fig. 3). Samples were acquired using a percussion device coupled with a Cobra TT model engine and cylindrical samplers 2 m long and 6 cm in diameter. Natural conditions allowed core sampling only up to a depth of 7.5 m. All cores were opened and described in the field, with most samples for laboratory processing collected at 20-cm intervals (or 10 cm in the case of core RR51-E).

In the field, the sedimentary facies were photographed and recorded on lithostratigraphic profiles. Facies description included lithology, texture, sedimentary structure and type of facies contact. The chronology was established using radiocarbon dating. Due to high sand content, the chronology was based on 18 samples of organic muds interbedded with the sands. The $^{14}\mbox{C}$ counting was performed with an accelerator mass spectrometry (AMS) device at the Beta Analytic and University of Arizona radiocarbon dating laboratories. Possible contaminants, including modern roots, were eliminated manually during pre-treatment. The organic matter was extracted using the laboratories' standard pre-treatment with acid-alkali-acid wash. Several rinses attempted to remove recent organic matter and ancient organic matter in the process of slow decomposition adsorbed in the sediments. Conventional $^{14}\mathrm{C}$ ages were calibrated to calendar years (cal a) BP using CALIB 6.0 and the INTCAL09 curve (Reimer et al., 2009).



Figure 2. Vegetation types characteristic of the study area. (A) Open vegetation covering the Viruá megafan. (B) Dense forest from areas surrounding the megafan. (C,D) Forest islands interspersed within open vegetation inside the megafan paleomorphology (C, aerial photograph; D, sketch C detailing the different floristic patterns).

As pollen data could not be obtained from the studied deposits, probably due to the dominantly sandy nature and oxidizing conditions. The paleovegetation was approached through δ^{13} C and, when possible, C/N. TOC and δ^{13} C analyses were performed on 271 samples at the Stable Isotope Laboratory from the Center for Nuclear Energy in Agriculture (CENA/USP) in Brazil. Laboratory procedures consisted in drying the sediments at 50 °C for 24 h. Each sample was grounded and subsamples of up to 70 mg were taken, depending on the amount of organic carbon present. In general, the TOC values of these samples are low (i.e. <2%; Fig. 4), as reported in many other Amazonian areas (e.g. Freitas et al., 2001; Miranda et al., 2009; Castro et al., 2010). This is mainly attributed to the prevalence of sandy lithologies rather than to organic matter degradation. On the other hand, the N amounts in the studied deposits were insufficient for TN and

NOOT

Figure 3. Physiographic map indicating the location of the cores taken within the Viruá megafan paleomorphology.

 $\delta^{15}N$ measurements. Exceptions are cores RR51-E and RR57-E, where TN content could be measured probably due to the greatest mud content. Both TN and $\delta^{13}C$ analyses were carried out using an elemental analyser connected to a mass spectrometer (ANCA-SL 2020 by Europa Scientific). Results are expressed in percentage of dry weight (total C and N) and as $\delta^{13}C$ with respect to the VPDB (Viena Pee Dee Belemnite) standard using the conventional δ (‰) notations, with analytical precision of \pm 0.1‰.

Sedimentary description and radiocarbon ages

The surface of the Viruá megafan consists of quartzose, moderately to well-sorted, very fine- to medium-grained sands, although coarse-grained sands are locally significant. These lithologies prevail also in the subsurface, although finergrained, silty and muddy lithologies are locally interbedded with the sand layers (Figs 5–7). A detailed analysis of sedimentary facies and interpretation of depositional processes



Figure 4. TOC distribution along the studied cores.





are presented in a seperate publication (Rossetti *et al.*, 2012b). However, a brief description of the main sedimentological characteristics is provided to give an overview of the depositional environments where the organic matter used for the isotope analysis was preserved.

Most of the sandy lithologies are graded into coarsening- or fining-upward units. The former are dominant and represented by several superposed cycles up to 4 m in thickness, where sands grade upward from very fine grained to either medium or coarse grained. Quartz granules and pebbles can be dispersed in the uppermost parts of the cycles. The top surfaces of the coarsening-upward sandy units are essentially sharp, while their lower boundaries are gradational into thin (i.e. <0.2 m), either massive or laminated silty or muddy facies, with a sharp lower unit boundary only in one location (i.e. in core RR66-F). In two cores derived from ecotone areas (cores RR51-E and RR57-E), these fine-grained lower units reach up to 3 m in thickness, resulting in coarsening-upward cycles up to 5 m thick. Muddy deposits from coarsening-upward cycles at the lower unit boundary of core RR55-O and between 1.5 and 3.0 m depth in core RR61-F display disperse quartz granules and pebbles, which increase in abundance upward. In the contemporary landscape, coarsening-upward cycles are associated with interchannel areas.

The fining-upward deposits consist of successions that grade upward from coarse- to fine-grained, silty and eventually muddy deposits. These cycles, up to 2 m in thickness, are characterized by sharp erosional bases overlain by quartz pebbles and granules. Fining-upward cycles occur at the bases of cores RR57-E, RR66-F and RR67-O, and are also interbedded with coarsening-upward cycles in cores RR55-O, RR61-F and RR69-O. Only one site characterized by a paleochannel morphology (i.e. RR61-F) was sampled, and it is represented by fining-upward cycles near the surface.

The ¹⁴C (AMS) dating of the cycles described above revealed ages of 23 402–24 201 to \sim 660 cal a BP (Figs 5–7; Table 1). However, Late Pleistocene ages were recorded only in the lower half of core RR51-E (i.e. between 19 478-20 088 and 23 402-24 201 cal a BP), and in the bottom of core RR62-F (i.e. 17 539-18 024 cal a BP). Upward in these cores, as well as in all other cores, the sediments display only Holocene ages. Core RR57-E is early Holocene, and the remaining cores are middle to late Holocene in age. In general, radiocarbon ages increase consistently as a function of depth. Two age inversions are present in cores RR51-E and RR57-E, with the former displaying an age of 19 544-20 167 cal a BP at a depth of 3.15 m and of 19 478–20 088 cal a BP at a depth of 3.55 m, and the latter having an age of 10 115-10 238 cal a BP at a depth of 4.00 m and of 9653-9960 cal a BP at a depth of 5.75 m. However, the ages in each of these cores are very close to each other, suggesting fast sedimentation in both locations in the cited periods.

Description of carbon isotope and C/N data

The δ^{13} C data range from -32.2 to -19.6%, but with nearly 60% of the data lighter than -26.5% (Figs 5–7). These values are within the range for C₃ forest vegetation plants of many Amazonian areas (e.g. Pessenda *et al.*, 2001), as well of other tropical areas worldwide (e.g. Boutton *et al.*, 1998). The frequency of enriched values increases consistently upward in the profiles, but only in cores collected from ecotone and open vegetated areas.

The δ^{13} C curves derived from areas of open vegetation display the most enriched values (Fig. 5). This is well illustrated

by core RR67-O, acquired in the central area of the megafan, and which shows δ^{13} C values between -27.1 and -20.7%. Cores RR69-O and RR55-O were collected from a site located at a marginal position, with the latter being closer to the surrounding rainforest. Their δ^{13} C values reflect their locations, with variations from -28.5 to -19.6% (mean-26.1%) and -28.3 to -21.3% (mean -26.7%) in cores RR69-O and RR55-O, respectively. Cores RR67-O and RR69-O show subtle changes to less negative values only in the last 0.1 and 0.3 m, respectively. With the exception of these depth increments, 14% (RR67-O) and 59% (RR69-O) of values in the remainder of the cores were lighter than -26.5%, with progressive enrichment after the middle Holocene (i.e. 3.4-2.9 m depth). Core RR55-O records this shift only above 0.4 m depth, while the remainder of its curve (83%) has values lighter than -26.5%.

The cores from forested areas show the most depleted values (Fig. 6). Comparing only these three forest cores, the most negative values occur in core RR61-F (-32.2 to -27.3%; mean–29.0‰), acquired in a rainforest outside the megafan. In this core, 100% of the δ^{13} C values are lighter than -26.6%, and up to 97% are lighter than -28%. The other two cores are from forested islands within the megafan, with core RR66-F being more marginal relative to core RR62-F, which is reflected by δ^{13} C values ranging from -28.9 to -26.5% (mean -27.3%) and from -28.5 to -25.7% (mean -26.7%), respectively. Comparing these two cores, 100% of the values of the most marginal cores are lighter than -26.5%, but only 3% are lighter than -28.5%. In the other core, 56% of the values are lighter than -26.5%. It

is also interesting that these two cores display curves with similar inflections toward lighter values near the surface, which is not observed in core RR61-F sampled in the outer megafan.

The ecotone cores (Fig. 7) derive from the central megafan deposits and, as expected, display δ^{13} C values generally intermediate between forest and open vegetation, ranging from -28.2 to -20.6‰ in RR51-E, -28.0 to -24.6‰ in RR57-E and -27.4 to -23.7‰ in RR58-E (Fig. 7). Core RR51-E, which is the only one to contain a continuous record since the Last Glacial Maximum (LGM), displays the highest range of variation, with a trend toward enriched δ^{13} C values from 19 751 to 19 781 cal a BP. Overall, all three ecotone cores display progressive enrichment upward, but with inflections toward slightly depleted values near the surface. The C/N calculated from cores RR51-E and RR57-E gives values ranging from 3.0 to 84.1, and from 1.0 to 20.0, respectively. In the first core, the highest values (i.e. > 44.1) occur in the first 1.5 m, while in the second the highest values (i.e. >19.4) are recorded only above a depth of 0.3 m.

Paleoenvironmental setting

The depositional paleoenvironments must be analyzed before interpreting the sources of organic matter preserved, and discussing their implications for determining the modern floristic distribution over the megafan. Indeed, depositional processes exert a large influence on the final concentration of organic matter in sediments, which are representative of either the local or the regional floristic composition, or both.



Figure 6. Lithostratigraphic profiles and distribution of δ^{13} C values along the cores from forested areas.

Copyright © 2012 John Wiley & Sons, Ltd.

J. Quaternary Sci., Vol. 27(8) 854-864 (2012)



Figure 7. Lithostratigraphic profiles and distribution of δ^{13} C values along the cores from ecotone areas.

As in the case of some classical examples of megafans (Assine, 2005; Gumbricht *et al.*, 2005; Sinha and Sarkar, 2009; Chakraborty *et al.*, 2010), the studied deposits were previously attributed to a megafan depositional system based on

geomorphological characteristics derived from remote sensing data (Zani and Rossetti, 2012). The sedimentary facies are compatible with this paleoenvironmental setting, as megafans consist of amalgamated fining- and coarsening-upward sands

Table 1. AMS ¹⁴C dating of samples derived from cores acquired along the studied megafan.

Lab. sample No.	Sample name	Depth (m)	δ ¹³ C (‰)	Age (¹⁴ C a BP)	Error	2σ range (cal a BP)	Mean calibrated age (cal a BP)
AA89117	RR51.5	0.45	-23.7	703	35	634–695	664
BETA275717	RR51.13	1.35	-22.7	4080	40	4526-4730	4628
BETA288712	RR51.26	3.15	-26.3	16 700	80	19 544–20 167	19 855
BETA288713	RR51.30	3.55	-27.3	16 670	70	19 478-20 088	19 783
BETA275718	RR51.39	4.45	-29.4	19 980	110	23 402-24 201	23 801
BETA296249	RR55.5	4.90	-23.5	6470	40	7317-7476	7396
BETA296250	RR57.1	0.15	-23.9	108	0.4	95–138	116
BETA296251	RR57.4	4.00	-26.1	9000	50	10 115–10 238	10 176
BETA296252	RR57.5	5.75	-25.6	8800	50	9653-9960	9806
BETA296255	RR61.3	1.40	-30.9	2810	40	2750-2878	2814
BETA296256	RR61.7	4.60	-25.2	3930	40	4243-4445	4344
BETA296257	RR61.9	7.00	-25.3	4680	40	5315-5477	5396
BETA309792	RR62.1	0.35	-27.6	105.8	0.4	96-137	116
BETA309793	RR62.4	5.95	-26.0	14 640	60	17 539-18 024	17 781
BETA309794	RR66.1	0.40	-27.7	100	30	31-138	84
BETA309795	RR66.2	1.90	-22.5	3130	40	3362-3443	3352
BETA296260	RR67.2	1.95	-25.1	5390	40	6173-6287	6230
BETA296261	RR69.2	3.85	-25.1	5400	40	6174–6292	6233

and, to a lesser extent, muds, representative of highly migratory channels, crevasse splays, terminal splays and, subordinately, floodplains (e.g. Stanistreet and McCarthy, 1993; Nichols and Fisher, 2007; Chakraborty and Ghosh, 2010).

All studied cores were acquired from the medial zone of the megafan, except for core RR61-F, which derives from its apex. In the medial location, most of the coarsening-upward sandy deposits can be attributed to episodic, high-energy overbank flows representative of crevasse splays that prograded into the floodplain areas. As a consequence, the fine-grained strata at the base of splay deposits are related to low-energy deposition of mud along the floodplain environments. The thicker muddy strata at the base of the crevasse splay deposits probably represent local small depressions or ponds on the floodplain. Mud deposits with dispersed quartz granules and pebbles that increase in abundance upward from cores RR61-F and RR55-O suggest mudflows/debris flows formed by gravitational processes in areas having at least a smooth slope. Sharp-based, fining-upward successions are interpreted as the record of waning flow conditions within channels.

Amalgamated, coarsening- and fining-upward deposits represent high-energy environments with overflow episodes of sand progradation over floodplains, as well as sand deposition within channels mobile enough to rework at least most of floodplain deposits. The sedimentary record of ancient pounds and floodplains has the potential to preserve organic matter produced by algae and freshwater phytoplankton, leading to typical δ^{13} C values of -20% (Meyers, 2003), which are equivalent to the mixed signal of C3 and C4 terrestrial plants. In this regard, the C/N value is useful to distinguish terrestrial sources of organic matter (i.e. C₃ and C₄ plants) from algae and phytoplankton (e.g. Wilson et al., 2005a,b). For the instance of the study area, potential input of external carbon is the Viruá catchment, which is the source of all sediments deposited in the megafan. However, the catchment area is relatively small ($\sim 2000 \text{ km}^2$), and developed in metamorphic and volcanic rocks characterized by dystrophic and weathered soil profiles, where contributions of allochthonous carbon are minor. Thus, we argue that the organic matter preserved in sediments within this environmental context might represent a mixture of local vegetation with the vegetation from the sediment's source area, in this instance the Guiana Shield. Despite the potential contribution of organic matter from areas outside the megafan, analyses of isotope and C/N data along the cores revealed that differences between sites also seem to reflect the influence of variation in local vegetation, as discussed in the following section.

Floristic reconstruction through time

An increasing number of publications has provided floristic reconstructions based on analyses of $\delta^{13}C$ and C/N measurements from organic matter preserved in Quaternary sediments (e.g. Freitas et al., 2001; Biedenbender et al., 2004; Lamb et al., 2006; Vidotto et al., 2007; Freycon et al., 2010). The interpretations provided by these authors are based on the assumption that the original organic matter has not been modified by any of the following factors: early biodegradation by aerobic microbes, biosynthesis of inorganic nitrogen (Meyers, 1997; Chen et al., 2008), grain size (Thompson and Eglinton, 1978; Keil et al., 1994), or post-depositional modifications during sediment burial (reviewed by Chen et al., 2008). Although these factors might complicate the use of δ^{13} C and C/N as geochemical signatures for paleonvironmental reconstructions, it has been stated that trends in these proxies remain intact and can be used with confidence to reconstruct ancient environmental settings (Wilson et al., 2005a,b).

The studied profiles show no random vertical distributions of the studied proxies. The values grade upward, being compatible with the modern floristic composition representative of each site (Fig. 8). The mean δ^{13} C values for sediment samples of $-21.2 \pm 1.8\%$ collected in the open vegetation sites, $-28.2 \pm 0.6\%$ in the forest sites and $-24.6 \pm 1\%$ in the ecotone sites are respectively consistent with the prevalence of C₄ over C₃ or C₃ over C₄ plant compositions at these sites. Therefore, values along individual cores are considered representative of the original organic matter composition sourced into the megafan's depositional setting at a certain core location.

In general, the values between -32.2 and -19.6%, with 60% above -26.5%, suggest the overall prevalence of organic matter derived from C₃ land plants and/or freshwater plants, but with a contribution from C₄ land plants. The combination of δ^{13} C and C/N data in cores RR51-E and RR57-E (Fig. 7) confirms that a portion of the organic matter is derived from land plants, and part comes from freshwater phytoplankton, with the importance of land plants increasing at shallower depths. The overall higher frequency of enriched values upward in the cores from ecotone and open vegetated areas is interpreted as resulting from increased contribution of C₄ plants over time. In addition, the trend toward enriched δ^{13} C values recorded from around 19 751 cal a BP in core RR51-E, the only one to contain a continuous record since the LGM, is also compatible with this suggested progressively increased C₄ plant contribution.

The δ^{13} C enrichment in the uppermost parts of the profiles is associated with the progressive establishment of the open vegetation on the megafan surface over time. Although the δ^{13} C of the modern vegetation of the study areas was not analysed, Poaceae and Cyperaceae dominating in other open vegetated areas of Amazonia display δ^{13} C values that are most often compatible with the C₄ photosynthetic pathway (Vidotto *et al.*, 2007).

It is important to mention that the δ^{13} C enriched values detected along profile RR51-E, which covers the LGM, could also be related to the lower levels of atmospheric CO₂ verified during glacial periods (Monnin *et al.*, 2001). The cold climate during this period favored C₄ plant expansion in several areas worldwide (Ehleringer *et al.*, 1997; Boom *et al.*, 2001), including tropical areas (e.g. van der Hammen, 1974; Absy *et al.*, 1991). However, a decrease of only about 0.3‰ in the carbon isotope of surface water and 0.35‰ in terrestrial organic carbon transferred to the ocean–atmospheric reservoir is

Figure 8. Relationship between δ^{13} C values and distance of the cores from the *Ombrophyla* forest that surrounds the megafan. The data fall into three clusters representative of forest, ecotone and open vegetation.



documented since the LGM (Hofmann *et al.*, 1999). Taking these studies into account, it is assumed that the changes in atmospheric CO₂ through time did not affect significantly the δ^{13} C values reported herein.

Except for core RR51-E, the records of increased C_4 plant contribution in the study area are not synchronous when data from all cores are compared. C_4 plant contribution started earlier in the cores from open vegetation than in the cores from the ecotone. Hence, the increased C_4 contribution in core RR67-O was initiated at an estimated age of nearly 6400 call a BP, while in cores RR69-O and RR55-O it is recorded at later estimated ages of 6000 cal a BP and less than 3000 cal a BP, respectively. In the ecotone cores (Fig. 7), this change is detected near the estimated age of 4000 cal a BP. The inflections toward slightly depleted values near the surface of the ecotone cores suggest that these areas were occupied by C_3 land plants very recently, i.e. only a few hundred years ago, as shown by the AMS ages.

Another interesting finding is that, contrary to the open vegetated and ecotone areas, the prevalence of only depleted values in cores from forested areas suggests either that vegetation remained unchanged through time or that, before forest establishment, the sites were dominated by aquatic environments with freshwater plants. The presence of the latter is suggested by the low depleted δ^{13} C and low C/N values from cores RR51-E and RR57-E (Fig. 7). Based on these results, it is possible that the depleted $\delta^{13}C$ values from the other cores might record also the contribution of freshwater plants. This statement is compatible with the sedimentological interpretation, which indicates the presence of numerous subaqueous environments associated with fluvial channels and floodplains. The fact that the core from the rainforest (i.e. RR61-F) in the outer megafan has 100% of values lighter than -26.6% and up to 97% lighter than -28‰ rules out any significant contribution of C₄ plants associated with past arid climate. This interpretation is also consistent with the generally light values from the other two cores (i.e. RR62-F and RR66-F) derived from forested areas inside the megafan deposit. It is interesting that, despite also being dominated by light values well below -26.5% which remained constant up to the surface, these two cores can be distinguished from core RR61-F, located in the megafan's apex (Fig. 7). The distinction is based on the slight δ^{13} C enrichment toward the megafan's central areas (i.e. from RR66-F to RR62-F), evidencing a lower influence of the surrounding rainforest. Even considering that these light values do not reflect C3 land plants, but rather aquatic plants or even C3 herbs, an important conclusion is that in the modern forested areas there was no contribution from C₄ land plants since at least the middle Holocene. The $\delta^{13}C$ curves from forested areas were also sensitive enough to reveal even small changes in vegetation patterns related to location within the megafan. Hence, the depleted δ^{13} C value trend in the cores closer to the megafan margin is related to an enhanced and/or longer influence of organic matter sourced from the surrounding rainforest.

Potential controls on floristic distribution

Combined with the modern distribution of vegetation over the Viruá megafan, the interpretations of sources of organic matter provide the basis for discussing potential controls on their distribution in the sediments. The main factor controlling plant distribution in Amazonia has been the subject of debate, and the main hypotheses have considered the influence of topography (Vormisto *et al.*, 2004), soil (ter Steege *et al.*, 1993), geology (Räsänen *et al.*, 1987; van der Hammen *et al.*, 1992) and climate (ter Steege *et al.*, 2003; Ruter *et al.*, 2004). In

addition, these patches of open vegetation have been interpreted as remnants of a vegetation cover formed due to increased aridity during the Late Pleistocene (Ledru et al., 2006) and early to middle Holocene (Freitas et al., 2001; Pessenda et al., 2001, 2004). Several other authors have related changes in Amazonia vegetation patterns during the late Quaternary to climate fluctuations during the Last Glacial (e.g. Absy et al., 1991; Behling and Hooghiemstra, 2000; Mayle et al., 2000; Freitas et al., 2001; Pessenda et al., 2001, 2004; Ledru et al., 2006), a hypothesis that conflicts with the proposal that the Amazonas basin was dominated by forest since the LGM (Colinvaux et al., 2000; Mayle et al., 2004; Mayle and Power, 2008). The replacement of rainforest by open vegetation over large areas (i.e. the forest refuge model of Haffer, 1969) has also been categorically refuted by many independent studies (Bush et al., 2004; Mayle, 2004; Pennington et al., 2004).

Numerous articles have highlighted the role of changes in the physical environment through time as the key determinants of vegetation patterns in Amazonia, as well as other tropical areas around the globe (e.g. van der Hammen *et al.*, 1992; Behling and Hooghiemstra, 2000; Maslin and Burns, 2000; Freitas *et al.*, 2001; Sifeddine *et al.*, 2001; Mayle and Power, 2008). The fluvial hydrology of Amazonia changed significantly as the climate varied from arid to progressively more humid after the LGM (e.g. Latrubesse and Ramonell, 1994; Latrubesse, 2002; Rigsby *et al.*, 2009; reviewed by Mertes and Dunne, 2007). An increase in humidity by up to 40% was proposed to have occurred in the Amazon basin after the Younger Dryas (Maslin and Burns, 2000).

The information presented here generally supports previous findings regarding the way sedimentary dynamics have influenced the distribution of vegetation types over a large area in northern Amazonia. However, our isotope data do not support the fact that these changes reflect primarily climate fluctuations, although this hypothesis should not be ruled out. This is because, differently from other Amazonian areas, this region currently displays a particular climatic regime, which is strongly influenced by the periodic dislocation of the ITCZ resulting from changes in the Atlantic meridional overturning circulation (Chiang and Bitz, 2005) and/or tropical air-sea interactions, such as the El Niño and La Niña events (Broecker, 2003). A monsoon-like circulation develops (Marengo, 1992; Grimm, 2003), resulting in better defined dry/wet seasons in this region than in other areas of the Amazonian lowlands, with increased drought coinciding with strong El Niño events in contrast to pronounced precipitation under the effect of La Niña events. Climate modeling for the Amazon basin suggests duplication of the monsoon intensity during the LGM relative to the present as a result of a reduction in annual rainfall by 25-35% (Cook and Vizy, 2006). Therefore, it is expected that the Viruá megafan might have been developed under a monsoonal regime with an even more extensive dry season than the present. Such climatic conditions could have favored the development of C₄ grasslands at least in some areas adjacent to the megafan.

A model for the evolution of the open vegetation in the study area can be proposed taking into account the sedimentary processes (Fig. 9). The δ^{13} C and C/N values do not support any shift in vegetation patterns over time that could have responded to climate change. We hypothesize that, previous to the megafan development, the study area might have been dominated by rainforest (Fig. 9A). As the megafan developed, the forest was limited to areas of non-sedimentation (Fig. 9B). Although a climatic influence might have played a role during change from forest to open vegetation in the middle to early late Holocene, a key point to consider is the restriction of the latter to the megafan depositional area. The megafan morphology





Figure 9. Proposed model for the origin of the open vegetation patch as a response to sedimentary dynamics associated with the evolution of the Viruá megafan. (A) Landscape dominated by forest prior to megafan development. (B) Sedimentary dynamics restricts the occurrence of forest to the areas surrounding the megafan. (C) As the megafan was abandoned, its surface was progressively covered by open vegetation (times increase from A to C, with C representing the present landscape). See text for further explanation.

clearly matches the open vegetation extent, which is in great contrast to surrounding areas of typically dense rainforest. Rather than coincidental, this is regarded as evidence for the influence of sedimentary dynamics on plant development over this specific area. This leads us to propose that the abandonment of the megafan system from the middle Holocene might have triggered the appearance of open vegetation over the study area (Fig. 9C).

Our isotope data show that the establishment of open vegetation occurred at different times depending on location over the megafan area, with a range from around 3000 to 6400 cal a BP. As sedimentation continued, areas located far from the surrounding rainforest, i.e. toward the central areas of the megafan deposits, were prone to inputs of organic matter derived from open vegetation, whereas the contribution of organic matter derived from arborous vegetation increased toward the areas located closer to the rainforest. This large time interval for the development of open vegetation within a given region minimizes the direct effect of climate solely as the main control on plant growth. In addition, a southward dislocation of the ITCZ during this time interval would arguably have brought humidity over Amazonian areas (Mayle et al., 2000). Greater humidity has been recorded in several Amazonian areas since the middle Holocene (Maslin and Burns, 2000; Pessenda et al., 2001; Sifeddine et al., 2001; Rossetti et al., 2004, 2005; Jacob et al., 2007; Cordeiro et al., 2011), which culminated with the expansion of the rainforest as we know it today. In addition, melting of the global ice volume during the transition from the last glacial phase to the current interglacial culminated with a mid-Holocene global rise in sea level of up to 5 m (e.g. Shackleton, 1988), with a consequent increase in humidity.

The trend toward a greater C₄ plant contribution recorded in core RR51-E could result from drier/less humid climates during and following the LGM. During this time interval, the tree canopy could have opened in many Amazonian areas, providing an opportunity for the development of C₄ plants. This interpretation is compatible with paleontological data derived from a central Amazonian location near Itaituba in the State of Pará, where a megafauna consisting of Haplomastodon waringi and Eremotherium laurillardi was determined to have ages of 15 290 (\pm 70) and 11 340 (\pm 50) ¹⁴C a BP, respectively (Rossetti et al., 2004); these species lived in open habitats such as arborous savanna (Cartelle, 1999). However, the prevalence in the studied deposits of land and aquatic C₃ plants during the Holocene attests to a landscape evolving under at least considerable humidity. Additionally, the increased C₄ plant contribution in this depositional environment took place while the region became increasingly humid in the mid to late Holocene, a process that culminated with the development of the modern wetland. Thus, it does not seem justified to associate the increase in C_4 vegetation to drier climatic conditions. On the contrary, as the environment became more humid, plant types changed from forest into open vegetation with an increased C_4 plant contribution. Therefore, although past climatic changes might have played a role, vegetation patches within the rainforest was influenced by changes in plant community due to sedimentary dynamics. Although further studies are still necessary to reconstruct the evolution of the depositional system in this area, climate might have had an indirect influence, contributing to increased sediment and water inflows into this area and thus the megafan advance during periods of high precipitation.

Conclusion

The times over which vegetation became established in different areas of the large patch of open vegetation we studied in northern Brazil were asychronous. They coincided with overall increased humidity, showing that the origin of C₄ plant types was most likely unrelated to past drier climatic episodes. Based on our results, we feel that caution should be exercised when using C₄ plants as a proxy to interpret directly arid climatic episodes during the late Quaternary in Amazonia. This study shows that the origin of the Viruá open vegetation patch was mostly influenced by the evolution of a large-scale depositional environment, recorded by a megafan system. Previous to the megafan deposition, rainforest might have dominated over the entire study area. Sedimentary processes limited the forest to the areas surrounding the megafan. However, as the megafan was progressively abandoned after the mid-Holocene, open vegetation dominated its surface. In addition, there are noticeable differences in the source of organic matter according to site location within the megafan deposit. Sediments located at the margins of the megafan show greater influence of organic matter derived from the surrounding rainforest, whereas deposits from the central megafan display higher influence of open vegetation. The results presented here might help to clarify the origin of large patches of open vegetation in other Amazonian areas displaying active sedimentary dynamics during the Late Pleistocene-Holocene.

Acknowledgements. We acknowledge the Research Funding agency of the State of São Paulo-FAPESP (Project #2010/09484-2 and doctoral grant 2009/00672-3) and the Brazilian National Council for Scientific and Technological Development for the financial support of this research and research fellowships. Logistical support during fieldwork was provided by CPRM – the Brazilian Geological Survey of the State of Roraima. Antonio Lisboa and Beatriz Lisboa from the ICM-Bio-Chico Mendes Institute for Biodiversity Conservation helped with fieldwork in Viruá National Park.

Abbreviations. AMS, accelerator mass spectrometry; ITCZ, Intertropical Convergence Zone; LGM, Last Glacial Maximum; TN, total nitrogen; TOC, total organic carbon.

References

- Absy ML, Cleef A, Fournier M, *et al.* 1991. Mise en évidence de quatre phases d'ouverture de la forêt dense dans lê sud-est de lAmazonie au cours dês 60.000 denières années. Première comparaison avec dautres regions tropicales. *Comptes Rendus* **312**: 673–678.
- Assine ML. 2005. River avulsions on the Taquari megafan, Pantanal wetland, Brazil. *Geomorphology* **70**: 357–371.
- Anderson AB. 1981. White-sand vegetation of Brazilian Amazonia. *Biotropica* **13**: 199–210.

- Anhuf D, Ledru M, Behling H, et al. 2006. Paleo-environmental change in Amazonian and African rainforest during the LGM. Palaeogeography, Palaeoclimatology, Palaeoecology 239: 510–527.
- Behling H, Hooghiemstra H. 2000. Holocene Amazon rainforestsavanna dynamics and climatic implications: high resolution pollen record from Laguna Loma Linda in eastern Colombia. *Journal of Quaternary Sciences* **15**: 687–695.
- Boom A, Mora G, Cleef AM, *et al.* 2001. High altitude C4 grass ecosystem in the northern Andes: relicts from glacial conditions. *Review of Palaeobotany and Palynology* **115**: 147–160.
- Boutton TW. 1996. Stable carbon isotope ratios of soil organic matter and their use as indicators of vegetation and climate change. In *Mass Spectrometry of Soils*, Boutton TW, Yamasaki S (Eds.) Marcel Dekker: New York; 47–82.
- Boutton TW, Archer SR, Midwood AJ, *et al.* 1998. δ¹³C values of soil organic carbon and their use in documenting vegetation change in a subtropical savanna ecosystem. *Geoderma* 82: 5–41.
- Bravard S, Righi D. 1989. Geochemical differences in an Oxisol– Spodosol toposequence of Amazonia, Brazil. *Geoderma* **44**: 29–42.
- Broecker WS. 2003. Does the trigger for abrupt climate change reside in the ocean or in the atmosphere? *Science* **300**: 1519–1522.
- Bush MB, Oliveira PE, Colinvaux PA, et al. 2004. Amazonian paleoecological histories: one hill, three watersheds. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology* **214**: 359–393.
- Biedenbender SH, McClaran MP. Quade. J et al. 2004. Landscape patterns of vegetation change indicated by soil carbon isotope composition. *Geoderma* 119: 69–83.
- Cartelle C. 1999. Pleistocene mammals of the Cerrado and Caatinga of Brazil. In *Mammals of the Neotropics. The Central Neotropics: Ecuador, Peru, Bolivia, Brazil.* Eisenberg J., Redford KH (Eds.). University of Chicago Press: Chicago; 27–46.
- Castro DF, Rossetti DF, Pessenda LCR. 2010. Facies, δ¹³C, δ¹⁵N and C/ N analyses in a late Quaternary compound estuarine fill, northern Brazil and relation to sea level. *Marine Geology* **274**: 135–150.
- Chiang JCH, Bitz CM. 2005. Influence of high latitude ice cover on the marine Intertropical Convergence Zone. *Climate Dynamics* **25**: 477–496.
- Chakraborty T, Ghosh P. 2010. The geomorphology and sedimentology of the Tista megafan, Darjeeling Himalaya: implications for megafan building processes. *Geomorphology* **115**: 252–266.
- Chakraborty T, Kar R, Ghosh P, *et al.* 2010. Kosi megafan: historical records, geomorphology and the recent avulsion of the Kosi River. *Quaternary International* **227**: 143–160.
- Chen F, Zhang L, Yang Y, *et al.* 2008. Chemical and isotopic alteration of organic matter during early diagenesis: evidence from the coastal area offshore the Pearl River estuary, south China. *Journal of Marine Systems* **74**: 372–380.
- Cloern JE, Canuel EA, Harris D. 2002. Stable carbon and nitrogen isotope composition of aquatic and terrestrial plants of the San Francisco Bay estuarine system. *Limnology and Oceanography* **47**: 713–729.
- Colinvaux PA, Oliveira PE. 2000. Palaeoecology and climate of the Amazon basin during the last glacial cycle. *Journal of Quaternary Science* **15**: 347–356.
- Colinvaux PA, Oliveira PE, Moreno JE, *et al.* 1996. A long pollen record from lowland Amazonia: forest and cooling in glacial times. *Science* **274**: 85–88.
- Colinvaux PA, Oliveira PE, Bush MB. 2000. Amazonian and neotropical plant communities on glacial time-scales: the failure of the aridity and refuge hypotheses. *Quaternary Science Reviews* **19**: 141– 169.
- Cook KH, Vizy EK. 2006. South American climate during the Last Glacial Maximum: delayed onset of the South American monsoon. *Journal of Geophysical Research and Atmosphere* **111**, D02110, DOI: 10.1029/2005JD005980.
- Cordeiro RC, Turcq B, Sifeddine A. 2011. Biogeochemical indicators of environmental changes from 50Ka to 10Ka in a humid region of the Brazilian Amazon. *Palaeogeography, Palaeoclimatology, Palaeoecology* **299**: 426–436.
- Ehleringer J, Bjorkman O, Helliker B. 1997. C4 photosynthesis, atmospheric CO₂ and climate. *Oecologia* **112**: 285–299.
- Freitas HA, Pessenda LCR, Aravena R, et al., 2001. Late Quaternary vegetation dynamics in the Southern Amazon Basin inferred from

carbon isotopes in soil organic matter. *Quaternary Research* 55: 39–46.

- Freycon V, Krencker M, Schwartz D, *et al.* 2010. The impact of climate changes during the Holocene on vegetation in northern French Guiana. *Quaternary Research* **73**: 220–225.
- Gribel R, Ferreira CAC, Coelho LS, et al. 2009. Vegetação do Parque Nacional do Viruá RR. Technical report, Boa Vista.
- Grimm AM. 2003. The El Niño impact on the summer monsoon in Brazil: regional processes versus remote influences. *Journal of Climate* **16**: 263–280.
- Gumbricht T, McCarthy TS, Merry CL. 2001. The topography of the Okavango Delta, Botswana, and its tectonic and sedimentological implications. *South African Journal of Geology* **104**: 243–264.
- Gumbricht T, McCarthy TS, Bauer P. 2005. The micro-topography of the wetlands of the Okavango Delta, Botswana. *Earth Surface Processes and Landforms* **39**: 27–39.
- Haffer J. 1969. Speciation in Amazonian forest birds. *Science* **165**: 131–137.
- Hofmann M, Broecker WS, Lynch-Stieglitz J. 1999. Influence of a $[CO_2(aq)]$ dependent biological C-isotope fractionation on glacial ${}^{13}C/{}^{12}C$ ratios in the oceans. *Global Biochemical Cycles* **13**: 873–883.
- Hartley AJ, Weissmann GS, Nichols GJ, et al. 2010. Large distributive fluvial systems: characteristics, distribution, and controls on development. *Journal of Sedimentary Research* **80**: 167–183.
- Horton BK, DeCelles PG. 2001. Modern and ancient fluvial megafans in the foreland basin system of the central Andes, southern Bolivia: implications for drainage network evolution in fold-thrust belts. *Basin Research* **13**: 43–63.
- Irion G, Müller J, Nunes de Melo J, et al. 1995. Quaternary geology of the Amazonian lowland. *Geo-Marine Letters* **15**: 172–178.
- Jacob J, Huang Y, Disnar JR, *et al.* 2007. Paleohydrological changes during the last deglaciation in Northern Brazil. *Quaternary Science Reviews* **26**: 1004–1015.
- Keil RG, Tsamakis E, Fuh CB, et al. 1994. Mineralogical and textural controls on organic composition of coastal marine sediments: hydrodynamic separation using SPLITT fractionation. Geochimica et Cosmochimica Acta 57: 879–893.
- Lamb AL, Wilson GP, Leng MJ. 2006. A review of coastal palaeoclimate and relative sea-level reconstructions using δ^{13} C and C/N ratios in organic material. *Earth-Science Reviews* **75**: 29–57.
- Latrubesse EM. 2002. Evidence of Quaternary palaeohydrological changes in middle Amazônia: The Aripuanã-Roosevelt and Jiparaná "fans". Zeitschrift für Geomorphologie **129**: 61–72.
- Latrubesse EM, Nelson BW. 2001. Evidence for Late Quaternary aeolian activity in the Roraima–Guyana Region. *Catena* **43**: 63–80.
- Latrubesse EM, Ramonell C. 1994. A climatic model for southwestern Amazonia at Last Glacial times. *Quaternary International* **21**: 163– 169.
- Latrubesse EM, Stevaux JC, Cremon EH, et al. 2012. Late Quaternary megafans, fans and fluvio-aeolian interactions in the Bolivian Chaco, Tropical South America. Palaeogeography, Palaeoclimatology, Palaeoecology 356–357: 75–88.
- Ledru M, Ceccantini G, Gouveia SEM, *et al.* 2006. Millenial-scale climatic and vegetation changes in a northern Cerrado (Northeast, Brazil) since the Last Glacial Maximum. *Quaternary Science Reviews* **25**: 1110–1126.
- Marengo JA. 1992. Interannual variability of surface climate in the Amazon basin. *International Journal of Climatology* **12**: 853–863.
- Martinelli LA, Almeida S, Brown IF, *et al.* 1998. Stable carbon isotope ratio of tree leaves, boles and fine litter in a tropical forest in Rondônia, Brazil. *Oecologia* **114**: 170–179.
- Maslin MA, Burns S. 2000. Reconstruction of the Amazon Basin effective moisture availability over the past 14,000 years. *Science* **290**: 2285–2287.
- Mayle FE. 2004. Assessment of the Neotropical dry forest refugia hypothesis in the light of palaeoecological data and vegetation model simulations. *Journal of Quaternary Science* **19**: 713–720.
- Mayle FE, Power MJ. 2008. Impact of a drier Early–Mid-Holocene climate upon Amazonian forests. *Philosophical Transactions of the Royal Society of London Series B* **363**: 1829–1838.
- Mayle FE, Beerling DJ, Gosling WD, et al. 2004. Response of Amazonian ecosystems to climatic and atmospheric carbon dioxide changes

since the last glacial maximum. *Philosophical Transactions of the Royal Society of London - Series B* **359**: 499–514.

- Mayle FE, Burbridge R, Killeen TJ. 2000. Millenial-scale dynamics of southern Amazonian rain forests. *Science* **290**: 2291–2294.
- Mertes LAK, Dunne T. 2007. Effects of tectonism, climate change and sea level change on the form and behaviour of the modern Amazon River and its floodplain. In *Large Rivers: Geomorphology and Management*, Gupta A (Ed.), John Wiley and Sons: London; 115–144.
- Meyers PA. 1994. Preservation of elemental and isotopic source identification of sedimentary organic matter. *Chemical Geology* **114**: 289– 302.
- Meyers PA. 1997. Organic geochemical proxies of paleoceanographic, paleolimnologic, and paleoclimatic processes. *Organic Geochemistry* **27**: 213–250.
- Meyers PA. 2003. Applications of organic geochemistry to paleolimnological reconstructions: a summary of examples from the Laurentian Great Lakes. *Organic Geochemistry* **34**: 261–289.
- Miranda MC, Rossetti DF, Pessenda LCR. 2009. Quaternary paleoenvironments and relative sea-level changes in Marajó Island (Northern Brazil): Facies, δ^{13} C, δ^{15} N and C/N. *Palaeogeography, Palaeoclimatology, Palaeoecology* **282**: 19–31.
- Monnin E, Indermühle A, Dällenbach A, et al. 2001. Atmospheric CO₂ concentrations over the last glacial termination. *Science* **291**: 112–114.
- Nichols G, Fisher J. 2007. Processes, facies and architecture of fluvial distributary systems deposits. *Sedimentary Geology* **195**: 75–90.
- Pennington RT, Lavin M, Prado DE, et al. 2004. Historical climate change and speciation: neotropical seasonally dry forest plants show patterns of both tertiary and quaternary diversification. *Philosophical Transactions of the Royal Society of London - Series B* 359: 515–537.
- Pessenda LCR, Boulet R, Aravena R, *et al.* 2001. Origin and dynamics of soil organic matter and vegetation change during the Holocene in a forest–savanna transition zone, Brazilian Amazon region. *The Holocene* **11**: 250–254.
- Pessenda LCR, Ribeiro AS, Gouveia SEM, et al. 2004. Vegetation dynamics during the late Pleistocene in the Barreirinhas region, Maranhão State, northeastern Brazil, based on carbon isotopes in soil organic matter. *Quaternary Research* **62**: 183–193.
- Räsänen ME, Salo JS, Kalliola RJ. 1987. Fluvial perturbance in the Western Amazon basin: regulation by long-term sub-andean tectonics. *Science* 238: 1398–1401.
- RADAMBRASIL Project. 1976. Folha NA–20 *Boa Vista: geologia, geomorfologia, pedologia, vegetação e uso potencial da terra.* Departamento Nacional de Produção Mineral: Rio de Janeiro.
- Reimer PJ, Baillie MGL, Bard E, *et al.* 2009. IntCal09 and Marine09 radiocarbon age calibration curves, 0-50,000 years cal BP. *Radiocarbon* **51**: 1111–1150.
- Rigsby CA, Hemric EM, Baker PA. 2009. Late Quaternary paleohydrology of the Madre de Dios River, southwestern Amazon Basin, Peru. *Geomorphology* **113**: 158–172.
- Rossetti DF, Toledo PM, Góes AM. 2005. New geological framework for Western Amazonia (Brazil) and implications for biogeography and evolution. *Quaternary Research* **63**: 78–89.
- Rossetti DF, Toledo PM, Santos HMM, et al. 2004. Reconstructing habitats in central Amazonia using megafauna, sedimentology, radiocarbon and isotope analysis. *Quaternary Research* **61**: 289–300.
- Rossetti DF, Bertani TC, Zani H, et al. 2012a. Late Quaternary sedimentary dynamics in Western Amazonia: implications for the origin of open vegetation/forest contrasts. *Geomorphology*, in press. [DOI: 10.1016/j.geomorph.2012.07.015]
- Rossetti DF, Zani H, Cohen MLC, et al. 2012b. A Late Pleistocene-Holocene wetland megefan in the Brazilian Amazonia. Journal of Sedimentary Geology, in press. [DOI: 10.1016/j.sedgeo.2012.09.015]
- Ruter A, Arzt J, Vavrus S, *et al.* 2004. Climate and environment of the subtropical and tropical Americas (NH) in the mid-Holocene: comparison of observations. *Quaternary Science Reviews* **23**: 663–679.

- Santos O, Nelson B, Giovannini CA. 1993. Corpos de areia sob leitos abandonados de grandes rios. *Ciência Hoje* **16**: 22–25.
- Servant M, Maley J, Turcq B, *et al.* 1993. Tropical forest changes during the Late Quaternary in African and South American lowlands. *Global and Planetary Change* **7**: 25–40.
- Shackleton NJ. 1988. Oxygen isotopes, ice volume, and sea level. *Quaternary Science Reviews* 6: 183–190.
- Sifeddine A, Marint L, Turcq B, *et al.* 2001. Variations of the Amazonian rainforest environment: a sedimentological record covering 30,000 years. *Palaeogeography, Palaeoclimatology, Palaeoecology* **168**: 221–235.
- Sinha R, Sarkar S. 2009. Climate-induced variability in the Late Pleistocene–Holocene fluvial and fluvio-deltaic successions in the Ganga plains, India: a synthesis. *Geomorphology* **3-4**: 173–188.
- Sinninghe Damsté JSS, Verschuren D, Ossebaar J, et al. 2011. A 25,000year record of climate-induced changes in lowland vegetation of eastern equatorial Africa revealed by the stable carbon-isotopic composition of fossil plant leaf waxes. *Earth and Planetary Science Letters* **302**: 236–246.
- Sioli H, Klinge H. 1961. Über Gewässer und Böden des Brasilianischen Amazonasgebietes. *Erde* **92**: 205–219.
- Stanistreet IG, McCarthy T. 1993. The Okavango Fan and the classification of subaerial fan systems. Sedimentary Geology 85: 115–133.
- ter Steege H, Jetten VG, Polak AM, *et al.* 1993. Tropical rain forest types and soil factors in a watershed area in Guyana. *Journal of Vegetation Science* **4**: 705–716.
- ter Steege H, Pitman N, Sabatier D, *et al.* 2003. A spatial model of tree α -diversity and density for the Amazon. *Biodiversity and Conservation* **12**: 1–19.
- Thompson S, Eglinton G. 1978. The fractionation of a recent sediment for organic geochemical analysis. *Geochimica et Cosmochimica Acta* **42**: 199–207.
- Tricart J. 1985. Evidence of Upper Pleistocene dry climate in northern South America. In *Environmental Change and Tropical Geomorphol*ogy, Douglas I, Spencer A (Eds.), Allen & Unwin: London; 197–217.
- van der Hammen T. 1974. The Pleistocene changes of vegetation and climate in tropical South America. *Journal of Biogeography* 1: 3–26.
- van der Hammen T, Duivenvoorden JF, Lips JM, et al. 1992. The Late Quaternary of the middle Caquetá area (Colombian Amazonia). *Journal of Quaternary Science* **7**: 45–55.
- Veloso HP, Rangel-Filho ALR, Lima JCA. 1991. *Classificação da Vegetação Brasileira, Adaptada a um Sistema Universal*. Instituto Brasileiro de Geografia e Estatística: Rio de Janeiro.
- Victoria RL, Fernandes F, Martinelli LA, *et al.* 1995. Past vegetation changes in the Brazilian Pantanal arboreal–grassy savanna ecotone by using carbon isotopes in the soil organic matter. *Global Change Biology* **1**: 165–171.
- Vidotto E, Pessenda LCR, Ribeiro A. 2007. Dinâmica do ecótono floresta-campo no sul do estado do Amazonas no Holoceno, através de estudos isotópicos e fitossociológicos. Acta Amazonica 37: 385– 400.
- Vormisto J, Tuomisto H, Oksanen T. 2004. Palm distribution patterns in Amazonian rainforests: what is the role of topographic variation? *Journal of Vegetation Science* **15**: 485–494.
- Zani H, Rossetti DF. 2012. Multitemporal Landsat data applied for deciphering a megafan in northern Amazonia. *International Journal of Remote Sensing* **33**: 6060–6075.
- Zani H, Assine ML, McGlue MM. 2012. Remote sensing analysis of depositional landforms in alluvial settings: method development and application to the Taquari megafan, Pantanal (Brazil). *Geomorphology* **161-162**: 82–92.
- Wilson GP, Lamb AL, Leng MJ, *et al.* 2005a. δ^{13} C and C/N as potential coastal palaeoenvironmental indicators in the Mersey Estuary, UK. *Quaternary Science Reviews* **24**: 2015–2029.
- Wilson GP, Lamb AL, Leng MJ, *et al.* 2005b. Variability of organic δ^{13} C and C/N in the Mersey Estuary, U.K. and its implications for sea-level reconstruction studies. *Estuarine, Coastal and Shelf Science* **64**: 685–698.