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Short Paper

The impact of climate changes during the Holocene on vegetation in northern French Guiana

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ABSTRACT

The impact of climatic changes that occurred during the last glacial maximum and the Holocene on vegetation changes in the Amazon Basin and the Guiana Shield are still widely debated. The aim of our study was to investigate whether major changes in vegetation (i.e. transitions between rainforests and C_4 savannas) occurred in northern French Guiana during the Holocene. We measured variations in the $\delta^{13}C$ of soil organic matter at eight sites now occupied by forest or savannah. The forest sites were selected to cover two regions (forest refugia and peneplains) which are thought to have experienced different intensities of disturbance during the latest Pleistocene and the Holocene. We found that none of the forest sites underwent major disturbances during the Holocene, i.e. they were not replaced by C_4 savannahs or C_4 forest savannahs for long periods. Our results thus suggest that tropical rainforests in northern French Guiana were resilient to drier climatic conditions during the Holocene. Nevertheless, geographical and vertical variations in the ^{13}C of SOM were compatible with minor changes in vegetation, variations in soil processes or in soil physical properties.

Introduction

Assessing the impact on tropical rainforests of a drier climate in the past is a major scientific challenge if we are to predict their response to present and future global climate change. The influence of climate changes during the last glacial maximum (LGM, ca. 20,000 years ago) and the Holocene (ca. the past 10,000 years) on vegetation changes in the Amazon Basin and the Guiana Shield are still widely debated. Some authors showed that some regions now covered by lowland rainforest remained relatively stable over these periods, and were simply enriched with mountain taxa (Behling, 1996; Colinvaux et al., 1996). In contrast, other authors showed that some rainforests were replaced by open forests with pioneer species (Charles-Dominique et al., 1998; Ledru, 2001), dry tropical forests, or savannahs (Van der Hammen 1974; Absy et al., 1991; Desjardins et al., 1996; Freitas de et al., 2001; Pessenda et al. 1998, 2001; Mayle and Power, 2008). The causes of heterogeneity in vegetation changes following drier conditions are still unknown, but appear to be correlated with local climatic and edaphic conditions, and the proximity of ecotones (Hooghiemstra and van der Hammen, 1998; Pessenda et al., 1998, 2001; Mayle and Power, 2008).

Many studies on vegetation changes during the latest Pleistocene and the Holocene have been conducted in the Amazon Basin, but far fewer in the Guiana Shield (Van der Hammen, 1963; Granville de, 1982; Ledru, 2001). Yet this region located in the northern part of the Amazon Basin, displays high species richness (Ter Steege et al., 2006), high above-ground biomass (Malhi et al., 2006) and large geographical gradients in floristic composition. To our knowledge, only one site in this region has been intensively studied (Charles-Dominique et al., 1998; Ledru, 2001) and vegetation disturbances were shown to have occurred during the Holocene. Furthermore, it has been suggested that this region underwent major vegetation disturbances during the latest Pleistocene (between 22,000 and 10,000 years ago) and rainforest refugia have been identified (Granville de, 1982; Tardy, 1998; Dutech et al., 2003).

The purpose of this study was to investigate whether existing forested areas in northern French Guiana experienced major vegetation changes during the Holocene. We assumed that forests located in the peneplain near present savannahs and with a high probability of vegetation disturbance during the latest Pleistocene (Granville de, 1982; Dutech et al., 2003) underwent such changes (i.e. replacement of rainforests by savannahs). In contrast, we assumed that forests located in regions described as forest refugia experienced no or only limited vegetation changes. To characterize possible past vegetation changes, we measured the variations with depth of the carbon isotope composition ($\delta^{13}C$) of soil organic

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matter (SOM). The use of SOM δ^{13}C enables the detection of vegetation changes between communities with varying proportions of plants with different photosynthetic pathways (C_3 vs. C_4 plants) (Boutton, 1996). This method has been successfully used to study major vegetation changes in Africa (Schwartz et al., 1992; Delegue et al., 2001; Guillet et al., 2001) and South America (Desjardins et al., 1996; de Camargo et al., 1999; Pessenda et al., 1998, 2001).

Materials and methods

Study area and vegetation

The study was carried out in northern French Guiana (Fig. 1). The mean annual temperature in French Guiana is around 26.5°C. Mean annual precipitation varies from 1500 mm in the southern and western parts to 4000 mm in the northeastern part. The regional

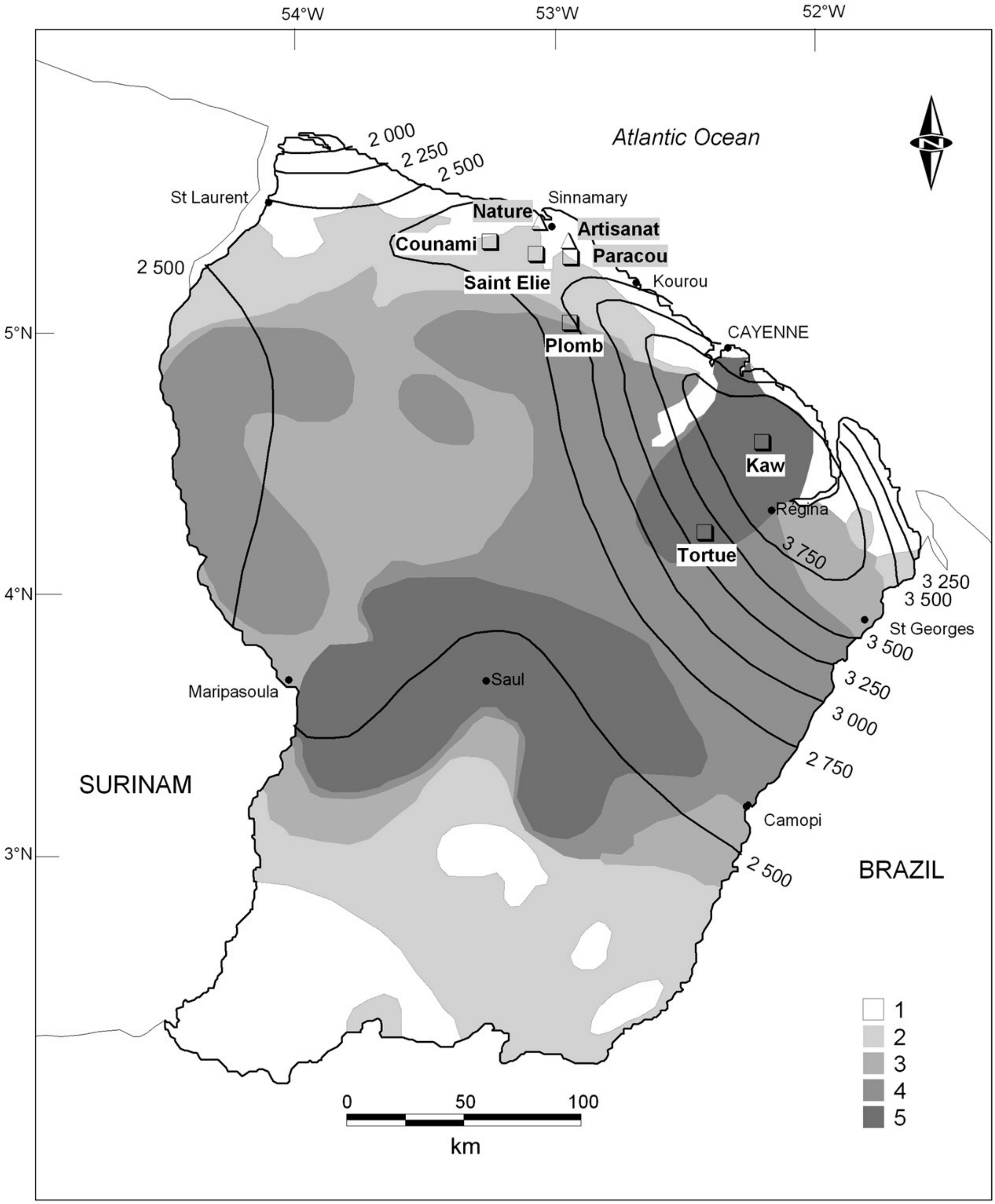

Figure 1. Map showing the location of the sites in French Guiana. The black lines are isohyetal lines (lines joining points of equal annual precipitation over the period 1961–1990). The font colors correspond to the levels of similar intensity of disturbances during the Pleistocene as described by Dutech et al. (2003) (from white = 1, highly disturbed, to dark = 5, no disturbance).

climate is tropical wet, characterized by an 8-month rainy season from December to July, interrupted by a short dry season in March, and by a long dry season with less than 100 mm per month from August to November (Groussin, 2001).

The eight sampling sites were located in three areas: (i) peneplain forests (Paracou, SaintElie, Plomb, Counami), (ii) forest refugia (Kaw, Tortue), and (iii) coastal plain savannahs (Nature, Artisanat) (Fig. 1 and Table 1). The average altitude was between 40 and 210 m asl at the peneplain forest sites, 200 m asl at the forest refugia site, and 6 m at the coastal plain savannah sites. Average annual rainfall was lower in the peneplain forest and at the savannah sites than at the forest refugia sites (3000 and 4000 mm, respectively). The clayey soils of forest sites were classified as Ferralsols or Acrisols, according to the IUSS Working Group WRB (2006). The sandy soils of the savannah sites were classified as intergrades between Ferralsols and Spodosols (Hoock, 1971).

The two savannah sites were dominated by Poaeceae, which are known to be mainly of the C_4 photosynthetic type. The floristic composition differed among the forest sites even though four botanical families were the most abundant (Caesalpiniaceae, Lecythidaceae, Sapotaceae, Chrysobalanaceae) (Paget, 1999; Sabatier and Molino, personal communication; Sabatier et al., 1997; Ter Steege et al., 2006).

Soil sampling and analytical methods

In 2004, ten pits were dug, eight at forest sites and two at savannah sites. At the forest sites pit depth was 210 cm, whereas at the savannah sites, it was only 60 cm, and 150 cm, due to the presence of groundwater. One pit was dug at each site, except at Paracou where three pits were dug to test for local spatial variability in the vertical δ^{13}C gradient. The shortest and the longest distances between the pits at Paracou were 550 m and 2770 m, respectively. The pits were dug at the top of small hills at all forest sites except at Plomb where the slope was 30%. When macroscopic charcoal particles were found in the pits, the depth was recorded. Generally, 15 soil samples were collected per pit at depths of (0–5 cm), (5–10 cm), (10–15 cm), (20–25 cm), (25–30 cm), (35–40 cm), (45–50 cm), (60–65 cm), (75–80 cm), (85–90 cm), (100–105 cm), (120–125 cm), (140–150 cm), (170–180 cm), and (200–210 cm). Soil samples were then dried at 40 °C to constant weight, and sieved at 2 mm. Root fragments were discarded by hand. Each sample was milled to obtain a homogenous powder.

The SOM δ^{13}C value of each sample was estimated at INRA Nancy, France, on a sub-sample of 3.10^{-3} g of dry soil powder using an isotope ratio mass spectrometer (Delta-S Finnigan Mat, Bremen, Germany). Natural ^{13}C abundance was expressed as δ^{13}C units (‰), by reference to the international standard PDB:

$$\delta^{13}\mathrm{C} = \frac{\left(R_{\mathrm{sample}} - R_{\mathrm{standard}}\right)}{R_{\mathrm{standard}}} * 1000,$$

where R_{sample} and R_{standard} are the ^{13}C/^{12}C ratio of the sample and standard, respectively. Analytical precision was ±0.1‰.

Radiocarbon analyses of SOM were carried out at the Poznań Radiocarbon Laboratory, Poland. Ages were expressed as ^{14}C yr BP (Before AD 1950) normalized to δ^{13}C of −25‰ PDB and in cal yr BP (CalPal Online, ver.1.5). Because of the continuous renewal of SOM, which is a mixture of young and old components, the ^{14}C age of SOM does not represent an absolute age of SOM, but its mean residence time (MRT). The calibrated ages thus have no real signification, we only give for comparison with previously published studies.

Results

δ^{13}C of SOM

At all sites, δ^{13}C values increased from the topsoil (0–5 cm) to the subsurface horizon (20–25 cm depth) by an average of 1.6‰ (Figs. 2A–D). This is due to the “Terrestrial Suess Effect” (Suess, 1955; Nadelhoffer and Fry, 1988; Boutton, 1996). δ^{13}C values of forest topsoils ranged from −28.8 to−27.7‰, typical values of C_3 plants. δ^{13}C values of savannah topsoils ranged from −14.6‰ to −15.8‰, typical of C_4 plants.

The two savannah soils displayed different δ^{13}C values and distribution profiles (Fig. 2A). The δ^{13}C profile at “Nature” was typical of a clear C_4 signature, whereas the profile at “Artisanat” was typical of a succession of old C_3 to recent C_4 vegetation (Schwartz et al., 1992).

δ^{13}C values of the forest soils ranged from −23.3 to −28.8‰ (Figs. 2B and C). Most profiles showed a general trend of ^{13}C enrichment with depth. Among these profiles, Paracou8 showed the least pronounced trend from –27.9‰ at 10 cm to −26‰ at 210 cm, and SaintElie showed the highest from –28.2‰ at 10 cm to –23.3‰ at 210 cm. At the Paracou site, the pattern of the three profiles was similar (Fig. 2D).

^{14}C dating of soil organic matter

Radiocarbon dates obtained from soil organic matter (SOM) all showed an increase in age along the profile (Table 2). At the maximum depth (200–210 cm), values of ^{14}C were highly variable and ranged from 4150 ^{14}C yr BP at Kaw to 14,620 ^{14}C yr BP at SaintElie.

Charcoal fragments

Macroscopic charcoal fragments were found in three profiles: Paracou2 at 20 cm and 50 cm, Paracou3 at 15 cm, and SaintElie at 150 cm.

Discussion

Period covered by this study

Considering that ^{14}C-dating of SOM reflects its mean residence time (MRT) (Guillet, 1994), we can conclude that our sampling strategy allowed us to cover at least a period from the Early–Mid-

Table 1
Characteristics of the study sites in French Guiana.[a]

Geographical area	Site	Vegetation type	DI	Latitude (N)	Longitude (W)	Elevation (m)	Soil type
Forest refugia	Kaw	Forest	5	4°34.23′	52°11.33′	190	Ferralsol
	Tortue	Forest	5	4°13.48′	52°24.60'	204	Ferralsol
Peneplain forest	Counami	Forest	1	5°20.25′	53°14.03′	56	Ferralsol
	Paracou2	Forest	1	5°16.75′	52°55.47′	50	Acrisol
	Paracou3	Forest	1	5°16.73′	52°55.75′	46	Acrisol
	Paracou8	Forest	1	5°15.38′	52°56.10'	45	Acrisol
	Plomb	Forest	3	5°01.63′	52°55.60'	210	Ferralsol
	SaintElie	Forest	1	5°17.52′	53°03.40'	75	Ferralsol
Coastal plain savannah	Artisanat	Savannah	1	5°20.63′	52°56.02′	6	Intergrade[b]
	Nature	Savannah	1	5°24.93′	53°02.73′	6	Intergrade[b]

[a] DI corresponds to the disturbance index described in Dutech et al. (2003).
[b] Intergrade between Ferralsol and Spodosol (after Hoock, 1971).

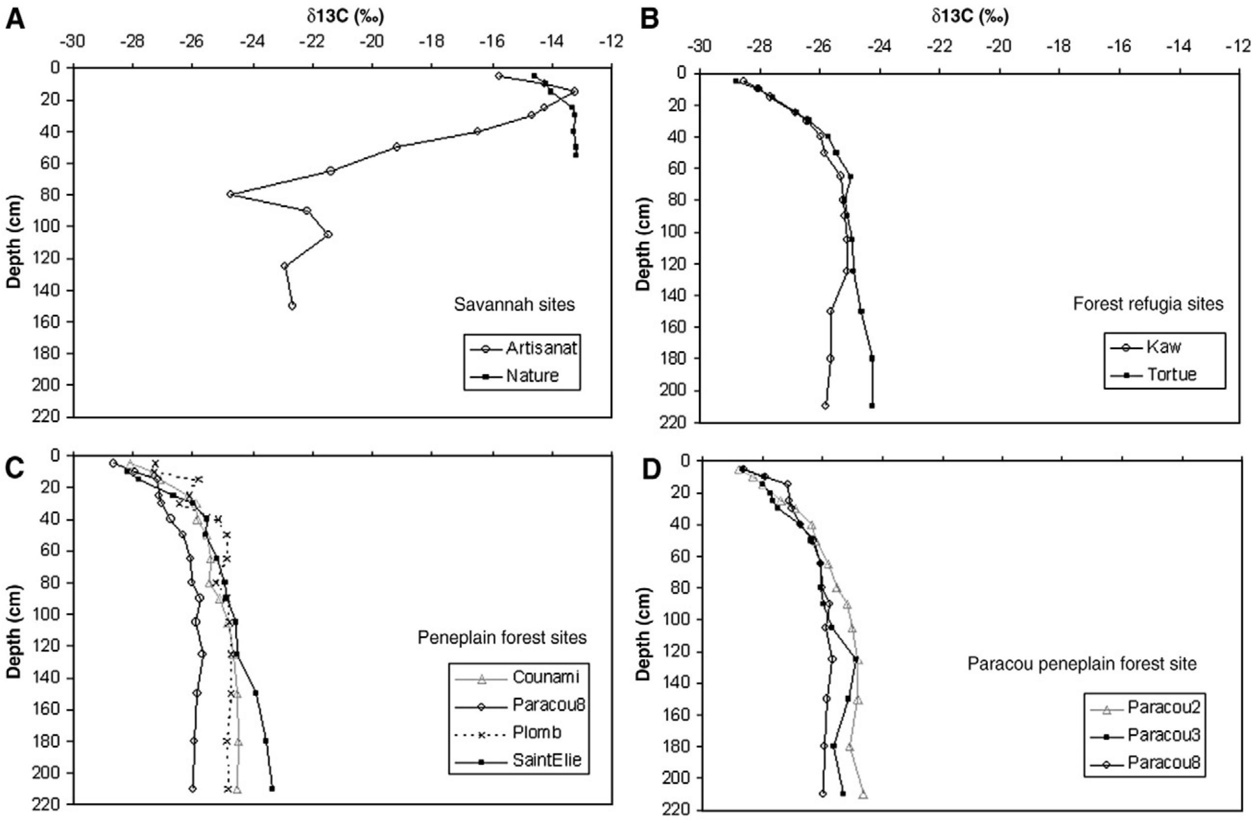

Figure 2. Variation in SOM δ^{13}C with soil depth at the study sites. (A) Savannah sites. Open circle = "Artisanat"; dark square = "Nature." (B) Forest refugia sites. Open circle = "Kaw," dark square = "Tortue." (C) Peneplain forest sites. Gray triangle = "Counami," open circle = "Paracou8," cross = "Plomb," dark square = "SaintElie." (D) Paracou peneplain forest site. The three profiles are located on Acrisols and are separated by about 2 km. Gray triangle = "Paracou2," dark square = "Paracou3," open circle = "Paracou8."

Holocene (around the past 8000–4000 years). For the northern part of Amazonia, it has been suggested that a long dry period ended around 8000 years ago (Carneiro et al., 2002; Mayle and Power, 2008), and was followed by a long wet period which experienced strong El Nino events between 3800 and 2800 years ago (Haug et al., 2001). Thus, if these changes led to major changes in vegetation (savannah vs. forest), we should be able to detect them through the ^{13}C signature of the SOM with depth.

No major disturbances of the forests of northern French Guiana

We originally assumed that in northern French Guiana, rainforests experienced different intensities of disturbance during the Holocene depending on their geographical location: forest refugia vs. peneplain forests. The major result of our study was the absence of SOM δ^{13}C values less negative than −23.3‰ at all forest sites (Figs. 2B–D). This suggests that none of these forest sites experienced major disturbances during the Holocene, i.e. they were not replaced by C_4 savannahs or C_4 forest savannahs for long periods. Consequently, we were not able to confirm any differences in vegetation changes between the two regions studied here.

For six out of eight profiles, either in forest refugia or in peneplains, the observed δ^{13}C profiles were typical of tropical rainforests in the Amazon Basin where no major changes in vegetation have been detected (Desjardins et al., 1991; Sanaiotti et al., 2002). These profiles correspond to the isotope signature of organic matter supplied to the soil over periods longer than the Holocene and coming from C_3 plants. The absence of colonization of these sites by C_4 savannahs during the Holocene is in agreement with the analysis of Hooghiemstra and Van der Hammen (1998), who concluded that rainforests located in regions where current annual rainfall is higher than 2500 mm were not replaced by savannahs during the drier climate periods of the LGM and the Holocene. As annual rainfall at our sites was all over 2500 mm, even when the driest scenario was simulated (i.e. a 40% reduction in current rainfall as discussed by Hooghiemstra and van der Hammen, 1998), the resulting reduced rainfall today would be more than 1500 mm and was thus not compatible with the replacement of tropical rainforests by savannahs. Our results are also in agreement with those of Mayle and Power (2008) who showed that forests in most parts of Amazonia appeared to be resilient to dry climatic conditions during the Early–Mid-Holocene. Previous taxonomic and molecular biology studies conducted in French Guiana – including at our study sites – concluded that these forests experienced major disturbances during the latest Pleistocene (Granville de, 1982; Dutech et al., 2003). Dutech et al. (2003) suggested that *Vouacapoua americana*, a shade-tolerant tree species of mature rainforest,

Table 2
Radiocarbon ages of soil organic matter collected at different soil depths of four profiles.

Profile	Laboratory number	Depth	Ages (^{14}C yr BP, 1σ)	Ages (cal yr BP, 1σ)
Counami	Poz-10049	20–25	40 ± 30	−30–110
	Poz-10050	75–80	3990 ± 35	4430–4510
	Poz-10052	120–125	4950 ± 40	5630–5720
	Poz-10053	200–210	8620 ± 50	9550–9650
Kaw	Poz-10117	20–25	635 ± 30	570–650
	Poz-10144	60–65	3795 ± 35	4120–4240
	Poz-10118	140–150	4095 ± 35	4550–4780
	Poz-10119	200–210	4150 ± 40	4620–4790
Paracou8	Poz-10130	20–25	50 ± 30	−30–130
	Poz-10131	60–65	3560 ± 35	3790–3900
	Poz-10132	120–125	5015 ± 35	5700–5860
	Poz-10134	200–210	7810 ± 60	8530–8680
SaintElie	Poz-10041	120–125	4510 ± 30	5090–5270
	Poz-10145	200–210	14,620 ± 90	17,560–18,320

underwent a major reduction in its distribution range and subsequent recolonization during the latest Pleistocene and the Holocene from refugia forests. Our observations do not contradict these results as these forests underwent minor changes in vegetation, i.e. the replacement of the mature rainforest by more open forest, which did not favor shade-tolerant species. Furthermore, as the period covered by our study mainly encompasses the Holocene, our observations suggest that the impact of Holocene climatic changes on vegetation changes in northern French Guiana may have been much lower than the impact of climatic changes in the latest Pleistocene.

Different $\delta^{13}C$ patterns are probably explained by minor vegetation changes and/or by pedogenic processes

Below 25 cm, the forest profiles displayed different patterns with depth. SaintElie and Kaw showed clear variations in δ^{13}C along the soil profile at 1.5 m and 1.3 m, respectively. At both sites, differences in SOM δ^{13}C with depth were great enough and repeated over a sufficient number of points for us to consider that these differences were not an artifact of the method. The fact that these variations were observed in both forest refugia and peneplain and that the other study sites did not display a similar pattern suggest that these processes may have occurred at local scales (a few square kilometers?), but not at large regional scales.

Ecological factors, pedogenic processes or soil physical properties can explain the geographical and vertical δ^{13}C pattern observed in soils (synthesis in Wynn et al., 2005).

Ecological factors, such as minor changes in vegetation during the Holocene, could explain the δ^{13}C pattern of SaintElie and Kaw, and we suggest two scenarios. The first scenario would have been the replacement of rainforests by tropical dry forests. This is supported by the fact that wet tropical sunlit leaves display an average of 3–4‰ less δ^{13}C than dry tropical leaves (Mooney et al., 1989; Sobrado and Ehleringer, 1997). The origin of these differences is related to higher water use efficiency (i.e., less negative leaf δ^{13}C values) in dry tropical species in environments with low soil water content (Farquhar and Richards, 1984; Ehleringer and Dawson, 1992). This scenario implies drier climatic conditions over long periods. Severe El Nino droughts occurred between 3800 and 2800 years ago off the Venezuelan coast at around 10°N (Haug et al. 2001), which is not far from French Guiana. Furthermore, major fire events occurred throughout the Guiana shield during the Holocene (Tardy, 1998; Hammond et al. 2006). The second scenario would have been a change in floristic composition within the rainforests. This is supported by the fact that huge interspecific variability in sunlit leaf δ^{13}C has been observed within a given tropical rainforest community (typically a range of 6–7‰ in a 1 ha forest) (Martinelli et al., 1998; Bonal et al., 2000). Consequently, a change in floristic composition within a community towards species with higher or lower δ^{13}C values could lead to a modification in the average δ^{13}C value of the ecosystem and of SOM. This change in floristic composition could be due to El Nino droughts (Slik, 2004; Newbery and Lingenfelder, 2009) and/or local anthropic disturbances. Changes towards a higher percentage of pioneer species in the ecosystem were previously observed at one site (“Les Nouragues”) in French Guiana between ca. 1520–1380 and 1060–860 years ago (Charles-Dominique et al., 1998; Ledru, 2001).

Pedogenic processes and soil physical properties could also explain the δ^{13}C pattern at SaintElie. In fact, increasing ^{13}C enrichment of SOM with depth is most frequently observed in well-drained, fine-texture soils and associated with an “old” SOM (Nadelhoffer and Fry, 1988, Trumbore 2000). At SaintElie, MRT at depth of 2.1 m was 14,620 ± 90 ^{14}C yr BP, i.e. much higher than at any other site at this depth (Table 2), and this clayey soil is well drained to a depth of at least 200 cm (Boulet, 1990). Thus, the less negative values observed at SaintElie at greater depths could be related to these pedogenic processes and not to minor changes in vegetation.

Conclusion

We found that the isotope signature of the eight profiles in forested areas showed no major changes in vegetation during the Holocene and that the rainforests at these sites were not replaced by C_4 savannahs during the Holocene. The profiles were selected in order to cover two regions (forest refugia and peneplain) in northern French Guiana which have been suggested to experience different intensities of disturbance during the latest Pleistocene and the Holocene. We were not able to reveal any differences in vegetation changes between these two regions. Our results thus confirm that wet tropical forests in northern French Guiana were resilient to drier climatic conditions during the Holocene.

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