Late Holocene Phytolith and Carbon-Isotope Record from a Latosol at Salitre, South-Central Brazil

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The reliability of paleovegetation records inferred from soil phytolith assemblages and SOM (soil organic matter) carbon isotope analysis was examined in light of previous pollen and charcoal reconstructions. The sampled latosol is located in south-central Brazil (Salitre), at a boundary between forest and cerrado. The derived mean age of phytoliths and SOM at each level is the result of a balance between continuous translocation and selective dissolution. It increases with depth in a regular, quantifiable fashion that allows paleoenvironmental interpretation. Phytoliths and SOM tracers first record a savanna phase, associated with the last Holocene long dry period occurring between ca. 5500 and 4500 yr B.P. Two periods of tree community development followed, between ca. 4000 and 3000 and after ca. 970 yr. B.P., leading to the present cerrado/forest association. The dry spell interrupted this trend about 970 ± 60 yr B.P. The second development of woody elements was contemporaneous with an increase in anthropogenic fires. Therefore, climate was more important than fires and human activities in constraining the growth of vegetation during the last nine centuries at Salitre. More generally, despite pedogenic processes, soil phytoliths and $\delta^{13}\text{C}$ values of the SOM may be accurate tracers of vegetation changes. © 1999 University of Washington.

Key Words: paleoenvironment; late Holocene; soil; phytolith; carbon isotope; charcoal; Brazil.

INTRODUCTION

Soils contain charcoal, soil organic matter (SOM), phytoliths, and human artifacts that are potentially useful for reconstructing paleoenvironments. Because soils are widespread, even in dry areas where lake sediments are often lacking, bioclimatic data obtained from them are particularly desirable for reconstructing past climates. However, the reliability of

paleoenvironmental interpretations of soil-particle sequences has been questioned (Cahen and Moeyersons, 1977). Particle distributions in soils are governed by four main pedogenic processes: translocation, dissolution (or mineralization), denudation, and colluviation (Johnson, 1990; Kelly *et al.*, 1991; Colin *et al.*, 1992; Boulet *et al.*, 1995; Alexandre *et al.*, 1997a). Particle translocation results from illuviation and/or fluid transportation in pores and from burrowing animals such as ants, termites, and worms, which bring to the surface materials from greater depths. Selective dissolution is related to the chemistry and surface area of the particles and to the stability of SOM/silica particles/clays aggregates (Bartoli and Wilding, 1980). Analysis of soil particles can provide useful paleoenvironmental information only if the age of the particles at each level can be reconstructed. In this paper, we present evidence that the mean age of phytoliths and SOM in the uppermost 2.6 m of a latosol in central southern Brazil increases with depth in a regular, quantifiable fashion. The mean age of particles at each level results from a balance between continuous translocation and selective dissolution. We then examine the reliability of paleovegetation records inferred from soil phytolith assemblages and SOM carbon-isotope analysis by comparison with pollen and charcoal data previously published. Finally, we reconstruct the movement of a boundary between forest and cerrado and its relation with paleofires during the late Holocene period.

STUDY AREA

The study area is located near Salitre de Minas (Minas Gerais State, Brazil, 19°S, 46°46'W) (Fig. 1). The climate is tropical, with an average annual rainfall of 1600 mm, a 4- to

FIG. 1. Map showing location of the study area in southeastern Brazil. After Ledru (1993).

5-month dry season, and an average annual temperature of 20°C. The area is located in a transition zone between the cerrado tree and tall grass savanna and the mesophytic semi-deciduous forest. Salitre is a 3.5-km-wide dolina-shaped depression lying at the center of an ultramafic-alkaline bedrock complex. The bottom of the depression lies at 980 m and is occupied by a peat bog from which the pollen data were obtained (Ledru, 1993; Ledru *et al.*, 1994, 1996). The slopes are covered by latosols developed at the expense of a 50- to 100-m-thick saprolite that overlies fenitized Proterozoic quartzites and shales. The soils extend as high as 1180 m. Denudation and colluviation do not affect these soils (Boulet *et al.*, 1995).

The profile sampled is developed on a slope, under a forest patch surrounded by the cerrado. It is vertically zoned into six horizons separated from one another by gradational boundaries (Fig. 2a). Evidence of high biological activity includes abundant roots, filled holes (tens of centimeters in diameter) caused by roots, or animal fecal pellets. The main minerals shown by X-ray analysis are kaolinite, gibbsite, goethite, hematite, and quartz. Pieces of charcoal (millimeters to centimeters in diameter) are scattered throughout the profile (Fig. 2b). They yield mean ^{14}C ages that increase with depth (Fig. 2 and Table 1). Their abundance-with-depth indicates that a number of fires occurred in the area between ca. 6000 and 3000 yr B.P. (Vernet *et al.*, 1994), in conjunction with a dry phase recorded by pollen (Ledru, 1993; Ledru *et al.*, 1994, 1996). Fifteen samples covering 5 to 20 cm of soil thickness were collected from 0 to 2.3 m depth.

PHYTOLITH AND SOM CARBON-ISOTOPE ANALYSIS

Phytoliths

Background. The basic grass phytolith classification defined by Twiss (1969, 1992) has shown that three grass sub-families are discriminated by the shape of the main short cell

phytoliths they produce: (1) cross and dumbbell morphotypes are produced in abundance by the Panicoideae, which consist mostly of C4 grass adapted to warm and wet environments; (2) saddle morphotype is produced in large amounts by the Chloridoideae, which consist of C4 grass adapted to warm and dry environments; (3) rectangular and circular morphotypes are produced in large amounts by the C3 Festucoideae. All grasses produce elongate, point-shaped, and fan-shaped morphotypes. This classification has been criticized because of multiplicity and redundancy of many grasses (Brown, 1986; Mulholland, 1989), which prevent the determination of plants on a species or genus level. However, many studies have also demonstrated that assemblage analysis is a very accurate way to characterize grass (Poaceae) communities of vegetation, which is not possible by pollen analysis (e.g., Kurmann, 1985; Piperno, 1988; Twiss, 1992; Fredlund and Tieszen, 1994; Piperno and Becker, 1996; Alexandre *et al.*, 1997a; Fredlund and Tieszen, 1997a,b). Moreover, Alexandre *et al.*, (1997b) demonstrated by modern and fossil phytolith assemblage analysis of sediments that the tree cover density of a given vegetation can be estimated with accuracy through the proportion of the circular rugose phytolith produced by dicotyledons. This morphotype appears relatively resistant to dissolution in latosols (Alexandre *et al.*, 1997a). Finally, Palmae are well indicated by the circular crenate morphotype (Piperno, 1988).

Thus, phytolith analysis appears to be especially accurate for tracing forest and grassland dynamics. However, their reliability as paleoenvironmental indicators in soils has been poorly studied (Kelly *et al.*, 1991; Piperno and Becker, 1996) because processes controlling phytolith distributions within soil profiles are barely understood.

Extraction and quantification. Following extraction of organic matter and iron oxides by wet chemical methods, phytoliths and charcoal were separated using heavy liquid from the 2- to 50- μm fraction (Kelly, 1990; Alexandre *et al.*, 1997a) and weighed. Charcoal particles were counted under the optical microscope and subtracted from the final weight.

Taxonomy and counting. Two hundred phytoliths were counted under the optical microscope (600 $\times$). Six morphotypes, with taxonomic significance previously described, were distinguished (Fig. 3a): (1) circular rugose, (2) circular crenate, (3) elongate, point-shaped, and fan-shaped, (4) cross and dumbbell, (5) saddle, and (6) rectangular and circular. The proportion of the woody flora in the reconstructed formations is inferred from the ratio $d:p$ where d = dicotyledon phytoliths and p = Poaceae phytoliths (Alexandre *et al.*, 1997b).

The modern assemblage extracted from the soil humic horizon is used as reference for the fossil assemblage interpretation. Its correlation with the surrounding vegetation is discussed on the basis of a wide investigation of cerrado grass phytoliths (Sendulsky and Labouriau, 1966; De Campos and Labouriau, 1969; Da Silva and Labouriau, 1970; Söndahl and

FIG. 2. (a) Soil profile (from Vernet *et al.*, 1994). (b) Charcoal distribution expressed in grams of charcoal per 10 liters of soil (from Vernet *et al.*, 1994). (c) Distribution of organic carbon. (d) SOM carbon isotope distribution. (e) Distribution of phytolith content. The broken line shows the main trend. (f) Distribution of phytolith surface features. (g) Phytolith diagram. Elongate category groups together elongate and fan- and point-shaped morphotypes. The abundance of each morphotype is expressed as the percentage of all phytoliths. Precisions of the data are expressed in the line thicknesses.

TABLE 1
Radiocarbon Dates of Charcoal from the Soil Profile and of Organic Matter (OM) from the Peat (Cores LC91/1 and LC3)

Lab number	Material	Depth (cm)	¹⁴ C age (yr B.P.)	Reference
OBDY 1254	Soil, charcoal	20–30	600 ± 40	Vernet <i>et al.</i> , 1994
OBDY 1255	Soil, charcoal	70–80	3160 ± 40	Vernet <i>et al.</i> , 1994
OBDY 1251	Soil, charcoal	100	3660 ± 90	Vernet <i>et al.</i> , 1994
OBDY 1252	Soil, charcoal	140–150	5840 ± 50	Vernet <i>et al.</i> , 1994
OBDY 1250	Soil, charcoal	180–190	6330 ± 30	Vernet <i>et al.</i> , 1994
OBDY 970	Peat (LC91/1), OM	14–20	970 ± 60	Ledru <i>et al.</i> , 1994
OBDY 551	Peat (LC3), OM	17–20	3060 ± 210	Ledru <i>et al.</i> , 1994
OBDY 556	Peat (LC3), OM	30–32	4350 ± 525	Ledru <i>et al.</i> , 1994
OBDY 555	Peat (LC3), OM	42–44	5560 ± 365	Ledru <i>et al.</i> , 1994

Labouriau, 1970). This investigation of cerrado grass contradicts the basic pattern of the Twiss classification on one point: C4 Panicoideae (e.g., *Trachypogon*, *Eriochloa*), which dominate the cerrado, and C4 Chloridoideae (e.g., *Chloris*, *Eragrostis*) yielded, in significant proportions, the rectangular and circular morphotypes. As no C3 Festucoideae are now widespread in the cerrado, rectangular and circular morphotypes cannot be correlated either with C3 Festucoideae or with another grass subfamily in this area.

In this study, phytolith data are discussed together with pollen data from the same area (Ledru, 1993; Ledru *et al.*, 1994, 1996).

SOM

Measurement of organic carbon content and SOM carbon isotope analysis. The organic carbon content of the <2-mm fraction was measured using a C–H–N analyzer. Precision of results is greater than 0.3%. The ¹³C/¹²C ratios of SOM ground, sieved, and homogenized to <200 μm were measured on a dry combustion elemental analyzer (CHN NA 1500, Carlo Erba) coupled to a Fisons SIRA 10 isotope ratio mass spectrometer (Girardin and Mariotti, 1991). Isotope abundance was expressed in δ¹³C versus PDB: δ¹³C‰ = [(¹³C/¹²C)_{sample} – (¹³C/¹²C)_{PDB}] / [(¹³C – ¹²C)_{PDB}] * 1000. Repeated δ¹³C measurements of a carefully ground and homogenized reference soil yielded a precision (1σ, 8 aliquots) of 0.06‰.

Background on SOM carbon isotopes. Carbon isotope fractionation between plant matter and atmospheric CO₂ associated with photosynthesis is smaller for C4 plants than for C3 plants. The average δ¹³C values of C3 and C4 plants are –26 and –12‰, respectively. The main control of SOM δ¹³C is litter input. However, numerous studies demonstrated that isotope fractionation during decomposition, humification, and differential preservation of ¹³C-enriched SOM components (e.g., Goh *et al.*, 1977; O'Brien and Stout, 1978; Nadelhoffer and Fry, 1988; Martin *et al.*, 1990; Mariotti, 1991), as well as recent variations in the ¹³C content of atmospheric CO₂ (Friedli *et al.*, 1986; Marino and McElroy, 1991), could cause ¹³C enrichment of forest SOM with depth. This ¹³C enrichment is always lower than 4‰, far smaller than the 14‰ difference between C3 and C4 plant litter. Therefore, given the time limits imposed by the turnover rate of SOM, it is possible to determine from the δ¹³C value of SOM if a change has occurred with time in the proportions of C3 and C4 plants in the overlying vegetation (e.g., Mariotti and Peterschmitt, 1994; Boutton, 1996; Desjardins *et al.*, 1996).

FIG. 3. (a) Microphotographs of the five morphotypes with taxonomic significance distinguished in this study: (1) circular rugose, (2) circular crenate, (3a) elongate, (3b) point-shaped, (3c) fan-shaped, (4) dumbbell, and (5) saddle. (b) Microphotographs of the two phytolith surface types: (1) with small etch pits (a few micrometers in diameter) and (2) with wide etch figures (about 10 μm in diameter).

RESULTS

Phytolith Data

Phytoliths (Fig. 2e) account for 0.1% of the <200- μ m fraction (dry weight) in the humic horizon (A_0), and tend to decrease below, interrupted by three peaks of abundance at 20–40, 80–90, and 140–190 cm depth. They represent 0.004% of the <200- μ m fraction at the bottom of the soil section.

Elongate, point-shaped, and fan-shaped morphotypes show two types of irregular surface features (Fig. 3b): small etch pits a few micrometers in diameter (type 1) and wide etch figures about 5–10 μ m in diameter associated with irregular and angular edges (type 2). Proportions of the two types of surface features on the fan-shaped phytoliths are illustrated in Figure 2f. Surfaces with wide etch figures increase from 0 to 100% from the top to the bottom of the soil section.

The phytolith diagram is presented as Figure 2g. Five zones may be discriminated on the basis of the *d:p* ratio and of the Poaceae phytolith spectra:

Zone 1 (230–200 cm). Ratios *d:p* at 230 and 200 cm, respectively, equal to 0.3 and 0.5. The Poaceae morphotypes are only represented by the elongate, point-shaped, and fan-shaped morphotypes.

Zone 2 (200–130 cm; charcoal ^{14}C dating according to Vernet *et al.*, 1994: 6330 ± 60 yr B.P. at 190–180 cm and 5840 ± 50 yr B.P. at 150–140 cm). Among Poaceae phytoliths, dumbbell and cross morphotypes appear, remaining under 3%; rectangular and circular morphotypes remain under 1.5%; saddle morphotype is present in weak proportion only at 150–140 cm. Ratio *d:p* varies between 0.3 and 0.8.

Zone 3 (130–40 cm; charcoal ^{14}C dating according to Vernet *et al.* (1994): 3660 ± 90 yr B.P. at 110–100 cm and 600 ± 40 yr B.P. at 30–20 cm). Ratio *d:p* stabilizes around 1 and 1.3. Grass phytoliths with precise taxonomic significance become more represented: cross and dumbbell morphotypes increase, fluctuating between 6 and 9%; saddle morphotype remains under 1.5%; rectangular and circular morphotypes increase between 3 and 6% but only from 110–100 cm.

Zone 4 (40–20 cm; charcoal ^{14}C dating according to Vernet *et al.*, 1994: 600 ± 40 yr B.P. at 30–20 cm). Ratio *d:p* remains equal to 1. The main feature of this zone is the significant increase of saddle morphotype, which surpasses 1.5% for the one and only time in the entire sequence.

Zone 5 (from 20 to 0 cm). Ratio *d:p* increases to 1.5. Among Poaceae phytoliths, cross and dumbbell morphotypes and rectangular and circular morphotypes account each for 5% of the total phytolith sum, whereas saddle morphotype abundance is less than 1.5%.

SOM Data

Organic carbon content (Fig. 2c) represents 20% of the <2 mm soil fraction (dry weight) in the organic A_0 horizon (0–5 cm). It decreases rapidly in the organo-mineral A_1 horizon (4–20 cm) to 2.7% of the <2 mm soil fraction between 20 and 40 cm depth. It decreases gradually downward, up to 1.02% of the <2 mm soil fraction at 220–230 cm depth. This profile does not show evidence of any buried soil or organic paleo-horizon.

The distribution of the $\delta^{13}\text{C}$ values of the SOM (Fig. 2d) shows three trends: (1) from the bottom of the profile up to 170–160 cm, it decreases from -19 to -22‰ ; (2) from 160 up to 40 cm, it stabilizes between -22 and -21.5‰ ; and (3) from 40 cm, it decreases rapidly to reach -28‰ in the organic horizon, which is in equilibrium with present litter inputs.

DISCUSSION

Pedogenic Processes Conducting to Phytolith and SOM Distributions

The decrease and stabilization observed with depth in the abundance of organic carbon is common to tropical and temperate soils. It may be modeled as a bicompartamental distribution, the result of particle translocation and mineralization (Jenkinson and Rayner, 1977; Parton *et al.*, 1987). A bicompartamental distribution assumes two pools of organic compounds. One pool is recycling rapidly and is in dynamic equilibrium. The input for that pool is litter at the top of the profile. With time, the organic matter in that pool is translocated downward and is mineralized, decreasing to trace levels at the bottom of the profile. The second pool is more stable and its translocation leads to a constant abundance distribution with depth. At the base of the soil profile, nearly all of the organic matter is in the stable pool. Paleoenvironmental significance of the SOM $\delta^{14}\text{C}$ and $\delta^{13}\text{C}$ mean values have commonly been discussed in terms of a similar bicompartamental model (O'Brien and Stout, 1978; Balesdent and Guillet, 1982). The general pattern of the phytolith distribution is somewhat similar to that of organic carbon. We interpret it as a bicompartamental distribution, by analogy with the bicompartamental model of distribution of the SOM. Such an interpretation has been already made to discuss a phytolith distribution in a latosol of Congo (Alexandre *et al.*, 1997a). It is here corroborated by the following points: if phytoliths surfaces with wide etch figures are more weathered than phytolith surfaces with small etch pits because of a longer residence time in the soil, their increase with depth suggests that (1) each phytolith assemblage is a mixing of young and old particles and (2) the mean residence time of phytolith assemblages increases with depth, which permits us to discuss the soil phytolith sequence as a paleoenvironmental record.

Phytolith and SOM Carbon Isotope Records

Because of the salitre depression shape, we will assume for this discussion that the main sources of allogenic particles found in the soil (e.g., phytoliths, charcoal, organic components) are local.

Phytolith record. The Poaceae phytolith assemblage of the humic horizon corroborates the dominance of tall C4 Panicoideae over short C4 Chloridoideae in the present vegetation. A *d:p* ratio of 1.5 results from the mixing between phytoliths that originated in both the forest patch and the surrounding cerrado. Using this modern assemblage as reference, five floral associations can be reconstructed from the phytolith sequence:

Zone 1 records a vegetation with abundant grasses. Woody elements are far less developed than today. The lack of short cell phytoliths characteristic of grass subfamilies would have involved grass phytolith production, dispersal, and/or preservation different than those found under modern conditions. This prevents further interpretation and indicates the limit of soil phytolith analysis.

Zone 2 records a grassland dominated by tall C4 grasses, with a density of tree or shrub cover far lower than the modern one. For the Holocene, only one savana phase, associated with warm and dry conditions, has been recorded at Salitre by pollen from the peat between 5560 ± 370 and 4350 ± 540 yr B.P. (Fig. 4a; Ledru *et al.*, 1994). It was contemporaneous with an increase in fires in the area (Vernet *et al.*, 1994). This latest and driest episode is well documented over tropical South America (Soubiès, 1980; Bradbury *et al.*, 1981; Absy *et al.*, 1991; Servant *et al.*, 1993; Ledru, 1993; Ledru *et al.*, 1996; Abbott *et al.*, 1997; Salgado-Labouriau *et al.*, 1997). Based on the assumption that phytoliths in the soil profile were produced by Holocene vegetation, the bottom of phytolith zone 2 would at least be younger than 5560 ± 370 yr B.P.

Zone 3 shows the development of trees and/or shrubs, which remain less abundant than today. This change may be related to the generation of conditions wetter than the previous ones (literature cited above) and to a decrease in fires (Vernet *et al.*, 1994). Pollen data (Fig. 4b) have also recorded such an increase of arboreal taxa between 4350 ± 540 and 3060 ± 210 yr B.P., followed by the development of a vegetation regarded as similar to the modern one (Ledru *et al.*, 1994). Phytolith data show, with more accuracy, that if the grass association was close to that of the cerrado, the present density of the tree cover was not reached yet.

Zone 4 records a slight decrease of trees (also corroborated by pollen data at 970 ± 60 yr B.P., Fig. 4b) and a brief but significant development of short C4 grasses. This might be related to a brief, very dry episode, which may have been contemporaneous with a mediaeval dry spell identified in Patagonia and California (Stine, 1994). The lack of data on modern paleoenvironmental changes in South America does not warrant further discussion of the significance of this event.

FIG. 4. Pollen diagrams from two cores from the Salitre peat (from Ledru *et al.*, 1994). (a) Core LC3. (b) Core LC91/1.

Following this dry episode, zone 5 records the return of conditions more favorable for the growth of vegetation. A rapid increase in the density of shrub and tree cover and a decrease in short C4 grass abundance led to the present association of forest and cerrado. Finally, the phytolith record from the soil is in good agreement with pollen data from the peat and strengthens the precision of the reconstruction of the most recent vegetation changes at Salitre.

SOM Carbon Isotope Record

At the top of the profile, $\delta^{13}\text{C}$ of the SOM is characteristic of a forest humic horizon (Mariotti and Peterschmitt, 1994; Desjardins *et al.*, 1996). Decay-with-depth of SOM in equilibrium with forest inputs (C3 plants), isotope effects associated with humification, differential SOM preservation, and recent $\delta^{13}\text{C}$ variations of atmospheric CO_2 imply a rapid but limited ^{13}C -enrichment of SOM in the topsoil, followed by a steady enrichment at lower depths, the whole enrichment being limited to 3 to 4‰ as generally observed (Boutton, 1996; Nadelhoffer and Fry, 1988; Mariotti and Peterschmitt, 1994). In agreement with this classic pattern, a 2-m-deep ferrallitic soil close to Salitre, assumed to be in equilibrium with forest inputs, shows a 2‰ enrichment, which is mostly located in the uppermost 40 cm (Desjardins *et al.*, 1991). The Salitre SOM $\delta^{13}\text{C}$ profile is different: the first ^{13}C shift in the uppermost 40 cm is greater than 7‰, while the second shift, in the 40 lowest cm, accounts for 3‰. These features indicate two major changes in the local flora: at the bottom of the section, the SOM $\delta^{13}\text{C}$ signature is the result of mixing between C3 and C4 plants, as in a tree savanna. A first increase of the density of shrubs or trees (both C3 plants) is recorded from 230 to 170 cm depth. A second step in the expansion of C3 plants is recorded above 40 cm depth, which led to the present association between forest and cerrado.

Finally, both phytolith assemblages and $\delta^{13}\text{C}$ values of the SOM clearly show evidence of two stages in the development of trees at Salitre after ca. 5000 yr B.P., but do so at different depths. SOM appear more rapidly translocated through lower horizons than phytoliths.

The correspondence between phytolith and pollen records permits us to place the first stage of tree expansion between 4350 ± 500 and 3060 ± 210 yr B.P. and the second after 970 ± 60 yr B.P. Comparison between time scales based on phytolith reconstruction and on charcoal ^{14}C dates (Fig. 2) show that phytoliths are translocated more rapidly than charcoal: for instance, the middle of the 4350 ± 500 to 3060 ± 210 yr time span recorded at 140–130 cm depth by phytoliths is recorded at 110–100 cm depth by charcoal (3660 ± 90 yr B.P.). This comparison also shows that if the first development of trees corresponds to the end of a long fire period, the most recent tree expansion corresponds to an increase in fires.

CONCLUSIONS

In South America, fires could be responsible for the late Holocene variations in the boundaries between forest and savanna (Soubiès, 1980; Desjardins *et al.*, 1996; Salgado-Labouriau *et al.*, 1997). Our results show that at Salitre, expansion of trees between ca. 4000 and 3000 yr B.P. corresponded to a decrease in fires, in agreement with Vernet *et al.*, (1994). This change led to the development of a vegetation association with less wood than the modern one. A dry spell, recorded by phytoliths at ca. 900 yr B.P., was not recorded by SOM $\delta^{13}\text{C}$ signatures because it was mainly expressed by a change among the C4 grasses. It was followed by expansion of trees and an increase in human-induced fires (Vernet *et al.*, 1994). This implies that climate was more important than fires in constraining the growth of vegetation during the last nine centuries at Salitre.

Finally, despite selective dissolution (or mineralization) in the studied soil, and mixing between young and old elements at each depth, phytoliths and $\delta^{13}\text{C}$ values of the SOM are accurate tracers of vegetation changes. As impact of tropical land surface conditions on the Holocene global climate variability has been hypothesized (Gasse and Van Campo, 1994), this study shows that soil phytoliths and SOM can provide information concerning the dynamics of the major tropical vegetation assemblages, which otherwise may be unavailable for regions that lack lake sediments.

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