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Environmental changes during the last millennium based on multi-proxy palaeoecological records in a savanna-forest mosaic from the northernmost Brazilian Amazon region

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ABSTRACT

The environmental changes and the dynamics of the savanna-forest mosaic, over the last 1050 years, have been reconstructed by pollen, charcoal, radiocarbon dating mineralogical and geochemical analyses of sediment cores taken from three different *Mauritia flexuosa* palm swamps in the northernmost part of the Brazilian Amazon region (northern state of Roraima). Studies on the relationship between the modern pollen rain and the regional vegetation provide additional information for the interpretation of the fossil pollen records. The fossil pollen assemblages and geochemical results indicate relatively wet climatic conditions throughout the recorded period. Despite these moist conditions, fires were frequent and are one of the reasons for the dominance of a grassy savanna instead of forest expansion in the study area. Considering the generally wet climatic conditions, these fires were most likely caused by human activities. Even today, fires hinder forest expansion into savanna areas. Sandy hydromorphic soils may also act as an edaphic control to maintain the current sharp boundary between forest and savanna ecosystems.

Key words: fire frequency, late Holocene, Roraima state-Brazil, vegetation dynamic.

INTRODUCTION

The northern and northeastern parts of the state of Roraima are located in the northernmost region of the Brazilian Amazon basin. The area is covered by extensive savanna surrounded by tropical forests and belongs to the so-called Rio Branco-Rupununi vegetation complex, which is the largest continuous block of savanna found in Brazilian Amazonia (Sarmiento and Monasterio 1975), covering about 41.000 km^2 in state of Roraima and extending into the territory of Guyana.

The history of the savannas located north of the Amazon basin, is still poorly known despite an increasing number of publications during recent years. Most of the records concerning the history of the savanna are located in the Llanos Orientales in

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Colombia (Behling and Hooghiemstra 1998, 1999, 2000, Berrio et al. 2000, 2002, Wille et al. 2003) and in the Gran Sabana of Venezuela (e.g. Rull 1992, 1999). The late Pleistocene and Holocene history of savanna ecosystems and environmental changes north and south of the Amazonian rain forest have been reviewed by Behling and Hooghiemstra (2001) and Behling (2002a). Pollen evidence from several savanna lake cores of the Llanos Orientales in Colombia, indicate an expansion of forest over savanna areas since about 4000 cal yr BP (Behling and Hooghiemstra 1998, 1999, 2000, Berrio et al. 2000). In the region of the Bolivian lowlands, an increase in precipitation probably facilitated an expansion of the Amazon rainforest, especially during the last 3000 years (Mayle et al. 2000, Burbridge et al. 2004). Isotopic studies carried out in the southern Brazilian Amazon basin (Pessenda et al. 1998, Freitas et al. 2001, Behling 2002b) suggest a similar forest expansion during the same period.

In the Roraima savanna region, only few palaeoenvironmental studies have been carried out (Absy 1979, Carneiro Filho 1991, Desjardins et al. 1996, Schaefer and Dalrymple 1996, Simões Filho 2000). Palynological studies are rare and geographically concentrated around the state capital Boa Vista and the eastern parts of the savanna region (e.g. Lake Caracaranã). The scarcity of data limits our ability to reconstruct the environmental and climatic history of the present-day landscape. According to Schaefer and Dalrymple (1996), this modern landscape is not in equilibrium with the current wet climatic conditions. Additional palaeoenvironmental records are needed to explain the coexistence of forest and savanna vegetation in reconstructing past environmental dynamics in this part of Amazonia.

Here we present multi-proxy records of the late Holocene environmental history of the savanna-forest transition area. *Mauritia*-rich palm swamps were used as an environmental archive. Our aim was to better understand the vegetation dynamics and to investigate the influence of climate, fire, humans and other factors by applying a multiproxy approach using pollen, charred particles, mineralogical and chemical analyses. In order to interpret the fossil pollen data, we also carried out studies on modern pollen rain-vegetation relationships.

ENVIRONMENTAL SETTING

The studied savanna-forest mosaic area is located in the northern part of state of Roraima, about 152 km northwest of the city of Boa Vista, between 3°12'00"– 3°42'00" N latitude and 61°06'00"– 61°34'05" W longitude (Fig. 1). Besides contrasting vegetation cover, the landscape also includes features such as dune fields, lateritic outcrops, stone lines and hundreds of shallow lakes in the low-lying plains. Three *Mauritia* palm swamp sites were selected for this study. The first site is located near Amajari city (AM), the second is located relatively close to the Uraricoera River (RU) and the third close to the indigenous land called Maloca do Boqueirão (MB). The climate of the area corresponds to tropical savanna climate, Aw according to the Köppen classification, with a mean annual temperature of 27 °C and an annual variation between 26 and 29 °C. The mean annual precipitation is about 1500 mm. The seasonal regime of precipitation defines a dry season between October and March and a wet season between April and September (Nimer 1991). Several soil types occur in the savanna-forest mosaic including lithosols, podzols and oxisols. The soils are strongly acidic (pH <5) and poor in nutrients especially in magnesium and phosphorus (Miranda 1998). The podzols are characterized by a sandy texture with low organic matter seasonally subjected to hydromorphic conditions and occur adjacent to palm swamps, while the laterite outcrops and oxisols are found on the more elevated dry terrains. All these soil types developed on rocks of the Cauarane Group consisting of metamorphic rocks, mainly quartzites and gneisses (Gaudette et al. 1996).

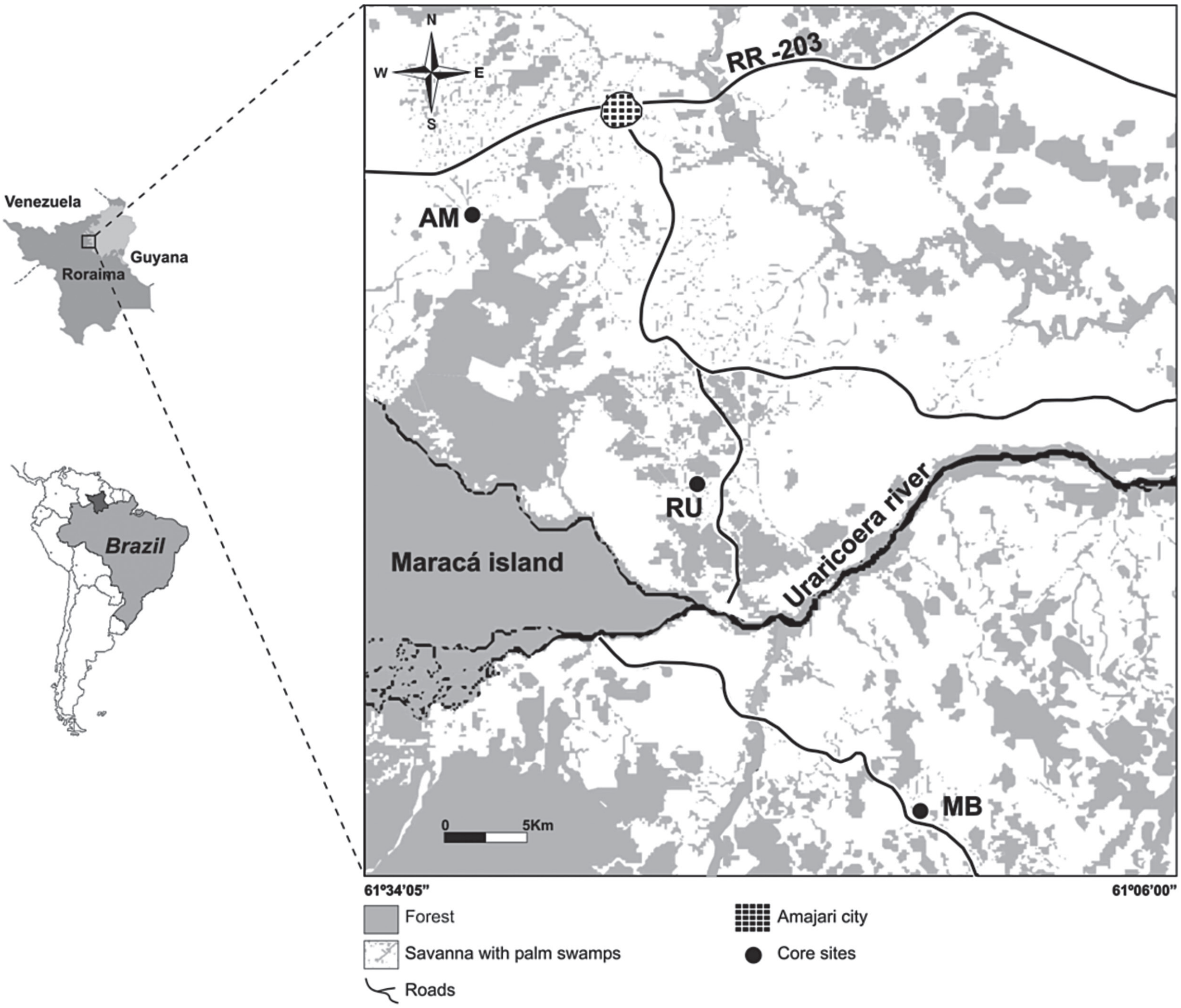

Figure 1- Map showing the study sites in the savanna-forest mosaic in state of Roraima, northern Brazilian Amazon region: AM - Amajari; RU - Uraricoera River; MB - Maloca do Boqueirão.

In the study area the savanna vegetation varies from grasslands at low-altitude (80-120 m a.s.l.) to open woodlands at higher altitudes (120 - 200 m a.s.l.). The herbaceous stratum is dominated by Poaceae (*Trachypogon plumosus, T. spicatus, Andropogon leucostachyus and Axonopus conduplicatus*) and Cyperaceae (*Rhynchospora nervosa, R. subplumosa, R. barbata, Bulbostylis conifera and B. lanata*), scattered with shrubs and small twisted trees with thick barks and sclerophyll leaves. Other frequent herbs are *Cassia flexuosa, Galactia jussiaeana, Merremia aturenesis* and *Eriosema crinitum* (Miranda and Absy 1997, Miranda 1998). The most common species in the shruby or arboreal stratum are *Curatella americana* (Dilleniaceae), *Byrsonima crassifolia* (Malpighiaceae), *Bowdichia virgilioides* (Fabaceae) and *Xylopia aromatica* (Annonaceae). Extensive palm swamps dominated by *Mauritia flexuosa* occur in the valleys and along the watercourses throughout the study area forming the so-called "*vereda*" like those well-known in central Brazil (Ferraz-Vicentini and Salgado-Labouriau 1996). The floristic composition of the palm swamps varies according to the successional stages. Therefore, the *Mauritia flexuosa* palm can occur as a single tree, associated with savanna herbs and grasses, or in denser stands coupled with gallery forest trees. Another forest formation is represented by islands of semi-deciduous forests situated on elevated terrains. A high number of palms such as *Attalea maripa, Astrocaryum* sp. and *Pyrenoglyphis* sp. belong to this forest type. The boundaries between savanna and forest are generally abrupt. Table I shows the floristic composition for savanna, gallery forest and semi-deciduous forest ecosystems according to regional inventories carried out by Miranda and Absy (1997) and Sette Silva (1993).

MATERIALS AND METHODS

SAMPLING AND DATING

The three studied sediment cores AM (Amajari), RU (Uraricoera river) and MB (Maloca do Boqueirão) were sampled in 50 cm-long sections using a Russian peat corer. The cores were stored under dark and cold (+ 4 °C) conditions. Four subsamples of bulk material (2 cm^3 volume) were taken for radiocarbon dating by Accelerator Mass Spectrometry (AMS) at the Beta Analytics Laboratory, USA. The ^{14}C dates were calibrated

TABLE I

List of savanna, gallery forest and semi-deciduous forest islands families and species according to field observations and regional inventories from Roraima savannas biome.

Savanna	Gallery Forest	Semi-deciduous Forest
Annonaceae	**Annonaceae**	**Anacardiaceae**
Xylopia aromatica	*Annona* sp	*Astronium* sp
Apocynaceae	*Duguetia guianensis*	*Spondias* sp
Himatanthus articulatus	*Xylopia* sp	**Annonaceae**
Bignoniaceae	**Apocynaceae**	*Duguetia* sp
Godmania esculifolia	*Himatanthus* sp	*Guatteria schomburgkiana*
Caesalpiniaceae	*Odontadenia geminata*	*Xylopia aromatica*
Cassia spp	**Arecaceae**	**Apocynaceae**
Stylosanthes guianensis	*Mauritia flexuosa*	*Aspidosperma* sp
Connaraceae	**Bignoniaceae**	*Himatanthus* sp
Connarus favosus	*Tabebuia uleana*	*Lacaellea arborescens*
Convolvulaceae	*Tanaecium jaroba*	**Arecaceae**
Evolvulus spp	**Burseraceae**	*Astrocaryum vulgare*
Ipomea assarifolia	*Protium aracouchili*	*Attalea maripa*
Merremia aturenesis	**Caesalpinaceae**	*Pyrenogliphis* sp
Cyperaceae	*Macrolobium acaciifolium*	**Bignoniaceae**
Bulbostylis spp	*Macrolobium multijugum*	*Tabebuia uleana*
Cyperus spp	*Macrolobium* sp	**Boraginaceae**
Eleocharis	*Swartzia laurifolia*	*Cordia* spp
Lagenocarpus spp	*Swartzia* spp	**Burseraceae**
Rhynchospora spp	**Chrysobalanaceae**	*Protium aracouchili*
Dilleniaceae	*Couepia* sp	*Tetragastris panamensis*
Curatella americana	**Clusiaceae**	**Caesalpinaceae**
Erythroxilaceae	*Clusia martiniana*	*Bauhinia ungulata*
Erythroxylum sp	*Clusia palmicida*	*Bauhinia* sp
Erythroxylum suberosum	*Vismia cayennensis*	*Hymenea courbaryl*
Erioucaulaceae	**Erythroxylaceae**	*Peltogyne* sp
Euphorbiaceae	*Erythroxilum* sp	*Senna multijuga*
Euphorbia brasiliensis	**Euphorbiaceae**	*Swartzia* sp
Euphorbia sp	*Acalypha* sp	**Convolvulaceae**
Sebastiania bidentada	*Alchornea* sp	*Turbina* sp

TABLE I (Continuation)

Savanna	Gallery Forest	Semi-deciduous Forest
Fabaceae	*Chamaesyce* sp	**Chrysobalanaceae**
Aeschynomene sp	*Mabea biglandulosa*	*Licania discolor*
Bowdichia virgilioides	*Mabea caudata*	*Licania* sp
Centrosema angustifolium	*Maprounea* sp	**Clusiaceae**
Crotalaria maypurensis	**Fabaceae**	*Vismia amazonica*
Desmodium spp	*Rhyncosia macrocarpa*	**Cucurbitaceae**
Eriosema sp	*Dioclea* sp	**Erythroxylaceae**
Indigofera sp	**Flacoutiaceae**	*Erythroxilum* sp
Rhynchosia sp	*Casearia negrensis*	**Fabaceae**
Flacourtiaceae	*Casearia* sp	*Centrolobium paraense*
Casearia sylvestris	**Lauraceae**	*Machaerium* sp
Gentianaceae	*Nectandra amazonua*	*Ormosia* sp
Coutoubea ramosa	**Lecythidaceae**	**Flacoutiaceae**
Schultesia sp	*Eschweilera pedicellata*	*Casearia sylvestris*
Lamiaceae	**Melastomataceae**	**Lauraceae**
Hyptis spp	*Clidemia bullosa*	*Mezilaurus itauba*
Lythraceae	*Miconia* sp	*Ocotea* spp
Cuphea ramulosa	**Mimosaceae**	**Lecythidaceae**
Malpighiaceae	*Acosmium* sp	**Malpighiaceae**
Byrsonima coccolobifolia	*Inga* sp	**Melastomataceae**
Byrsonima crassifolia	*Pithecelobium cauliflorum.*	*Miconia* sp
Byrsonima verbascifolia	*Pithecelobium marginatum*	**Mimosaceae**
Malvaceae	*Pithecelobium* sp	*Anadenanthera peregrina*
Sida spp	**Moraceae**	*Enterolobium schomburgkii*
Melastomataceae	*Brosimum lactescens*	**Monimiaceae**
Clidemia rubra	*Ficus* sp	*Siparuna guyanensis*
Miconia rubiginosa	**Myristicaceae**	**Moraceae**
Tibouchina aspera	*Virola* sp	*Brosimopsis* sp
Mimosaceae	**Myrtaceae**	**Myrtaceae**
Mimosa microcephala	*Eugenia* sp	*Eugenia* sp
Myrtaceae	*Myrcia* sp	*Myrcia* sp
Eugenia sp	**Olacaceae**	*Psidium* sp
Psidium guianense	*Heisteria acuminata*	**Piperaceae**
Ochnaceae	**Polygonaceae**	*Piper* sp
Ouratea sp	*Polygonum* sp	**Polygonaceae**
Onagraceae	**Rubiaceae**	*Coccoloba latifólia*
Ludwigia nervosa	*Duroia kotchubaeoides*	**Rubiaceae**
Ludwigia sp	*Faramea breviflora*	*Alibertia* sp
Polygalaceae	*Genipa americana*	*Duroia* sp
Polygala spp	**Sapindaceae**	*Faramea* sp
Poaceae	**Sapotaceae**	**Rutaceae**
Andropogon spp	*Matayba guianensis*	*Zanthoxylum* sp
Aristida spp	*Pouteria* sp	**Sapindaceae**
Axonopus spp	**Simaroubaceae**	*Coupania rubiginosa*
Mesosetum sp	*Simarouba amara*	**Sapotaceae**
Panicum spp	**Styracaceae**	*Matayba guianensis*
Paspalum spp	*Styrax guianensis*	*Pouteria venosa*
Trachypogon spp	**Tiliaceae**	**Simaroubaceae**
Proteaceae	*Mollia* sp	*Simarouba amara*
Roupala montana	**Vitaceae**	**Violaceae**

TABLE I (Continuation)

Savanna	Gallery Forest	Semi-deciduous Forest
Rubiaceae	*Cissus erosa*	*Amphirrox* sp
Borreria spp		**Vochysiaceae**
Palicourea rigida		*Vochysia* sp
Randia formosa		
Perama hirsuta		
Tocoyena sp		
Solanaceae		
Solanum sp		
Sterculiaceae		
Melochia spp		
Turneraceae		
Piriqueta duartiana		
Turnera sp		
Xyridaceae		
Xyris laxifolia		

using Calib 6.0 (Stuiver and Reimer 1993) and the Intcal09 calibration curve in order to calculate calendar ages.

In order to interpret the fossil pollen information from the study area, sediment surface samples obtained from different formations (savanna, *Mauritia* palm swamp with gallery forest, semi-deciduous forest island) were analyzed for modern pollen rain. A total of 17 samples consisting of 2 cm of surface sediment were taken in proper wet locations over about an area of 1.8 km^2 close to site AM. Six samples (1 to 6) were collected along the studied AM palm swamp where a gallery forest occurs (here referred as *Mauritia* swamp forest). Samples 7 to 10 were taken from a nearby forest island, and the remaining seven samples (11 to 17) from the surrounding grass-dominated savanna swamps (Fig. 2).

The pollen rain results were initially compared among themselves in order to recognize the pollen signal of different vegetation sites and then afterwards compared with regional floristic inventories carried out in the savanna and forest systems.

MINERALOGICAL AND CHEMICAL ANALYSIS

For mineralogical analysis, samples were taken along the cores at intervals of 5 cm. The samples were dried under room temperature and then afterwards milled to a powder texture. Mineral identification was carried out by X-ray diffraction (XRD) using a PANalytical, X'PERT PRO MPD model PW 3040/60®, cobalt anode (Kα1 1,78901 Ǻ).

Core AM was submitted to the non-destructive XRF scanning chemical analysis (major elements) using an ITRAX core scanner (Croudace et al. 2006) at the Institute of Geography (GEOPOLAR), University of Bremen. This instrument allows the simultaneous acquisition of semi-quantitative element concentrations at high spatial resolution. Compositional variations measured at a stepsize of 5 mm (Mo X-ray tube, 30 kV, 30 mA, 10s count time) are given in total counts (element peak area).

POLLEN AND CHARCOAL ANALYSIS

For pollen analysis, the cores were sampled at 2.5 cm intervals along the cores AM and MB and at 5 cm intervals along the core RU. All samples, including surface samples, were processed using standard pollen analytical methods applying hydrofluoric acid (HF) treatment and acetolysis (Faegri and Iversen 1989). For calculations of pollen concentration (grains/cm^3) and influx (grains/cm^2/yr) of the cores, tablets of *Lycopodium clavatum* spores

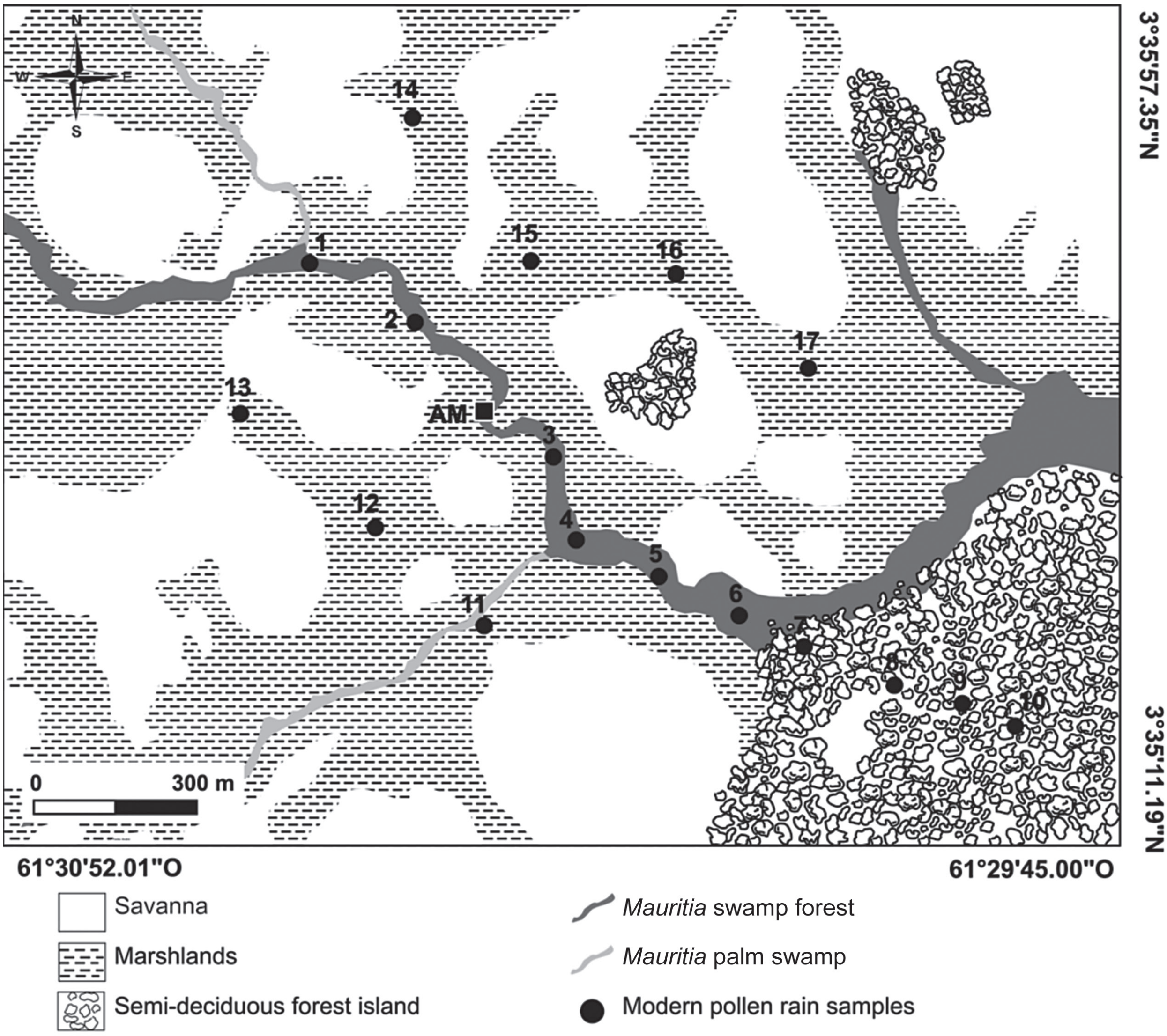

Figure 2 - Distribution of the modern pollen surface samples (1-17) around the AM site.

were added as an exotic marker. Due to the general over-representation of *Mauritia flexuosa* pollen, a minimum sum of 500 pollen grains was counted for each sample. The pollen sum includes pollen of trees, shrubs and herbs. Aquatic pollen, spores of pteridophyta and remains of algae were counted and quantified as percentages of the pollen sum.

The identification of pollen and spores is based on published pollen atlases and keys (Colinvaux et al. 1999, Roubik and Moreno 1991) and the reference collections of the third author, kept at the Department of Palynology and Climate Dynamics, University of Göttingen, containing approximately 3000 neotropical taxa. Identified pollen and spores were classified in ecological groups based on the vegetation information by Marchant et al. (2002), the floristic inventory of Roraima forests (Sette Silva 1993) and savanna regions (Miranda and Absy 1997) and also local observations during the fieldwork. TILIA®, TILIAGRAPH® and CONISS® were used for data calculation, illustration and cluster analysis (Grimm 1987). The microscopes slides are deposited in the Laboratório de Solos e Biogeografia of the Universidade Federal do Tocantins.

In order to reconstruct local fire events, charred particles (5–150 μm) were counted on the same pollen slides and calculated as charcoal concentration (particles/cm^3) and accumulation rate (particles/cm^2/yr).

RESULTS

CHRONOLOGY AND SEDIMENTOLOGY

The results of the AMS radiocarbon dating are shown in Table II. The chronological control for the AM core is provided by two AMS radiocarbon dates. The basal age of this core (95-93 cm core depth) indicates late Holocene deposits with an age of ca. 1050 cal yr BP. The second dated sample (50-48 cm core depth) has an age of about 820 ca yr BP. The basal age of the MB core (49-47 cm core depth) is dated to ca. 600 cal yr BP while a radiocarbon date from RU basal sediments (47-45 cm core depth) has a modern age (-463 ± 40 yr BP).

The lower core part between 95 and 52 cm of AM consists of dark grey, silty sand, intermixed with sandy layers rich in macroscopic plant debris. From 52 to 15 cm, the sediment consists of light grey, silty clay without plant debris becoming darker and enriched in leaves fragments and roots at the uppermost 15 cm depth. The 47 cm long core RU is formed by dark grey, clayey silt, rich in macro plant debris. The 50 cm long core MB is composed of light grey, compact silt. The reached substrata of all three cores consist of coarse sandy material devoid of pollen.

TABLE II
Radiocarbon and calibrated dates for the studied cores.

Laboratory Code	Samples	Depth (cm)	^{14}C yr BP	Calibrated age in years BP	Average in cal yr BP
Beta-269801	AM	48-50	950 ± 40	740 - 900	820
Beta-269802	AM	92-94	1170 ± 40	930 - 1170	1050
Erl-12838	MB	47-49	653 +/- 57	530 - 670	600
Erl-12840	RU	45-47	-463 ± 40	Modern	Modern

The main mineralogical components of the sediments are quartz and kaolinite. Sillimanite and muscovite also are present in small amounts as well as feldspars such as microcline and albite (Fig. 3). All these minerals have been identified in neighboring podzols and oxisols. Feldspars, sillimanite and muscovite, as well as quartz, are the main components of the regional bedrock formed by metamorphic rocks.

The element variations along core AM are illustrated in Fig. 4. No major compositional changes could be detected based on the distributions of the major elements K, Ca, Ti, Mn, and Fe. Low count rates in combination with a high scatter for Si and Al, make much difficult a conclusive evaluation of these elements. However, slight variations in K and Ti as well as in the ratios of incoherent to coherent scattering (inc/coh) and Fe/Ti, allow one to distinguish three main zones in core AM that are consistent with the identified palynological zones except for the subdivision of the zone AM-I in two subzones (AM-Ia and AM-Ib) (Fig. 4). Some elements exhibit rather large shifts at the position of the section break (e.g. Ti). This is possibly being caused by a matrix effect (such as somewhat drier sediments at the section end due to preferential dewatering). As there is no visual change in the sediment, these shifts cannot be interpreted in a palaeoenvironmental context.

Elemental counts for K and Ti are highly correlated. These elements are commonly regarded as proxy for minerogenic input (Enters et al. 2010). Potassium (K) is bound in micas and feldspars, whereas titanium (Ti) commonly occurs in heavy minerals such as ilmenite ($FeTiO_3$) or rutile (TiO_2). There is an increasing trend from

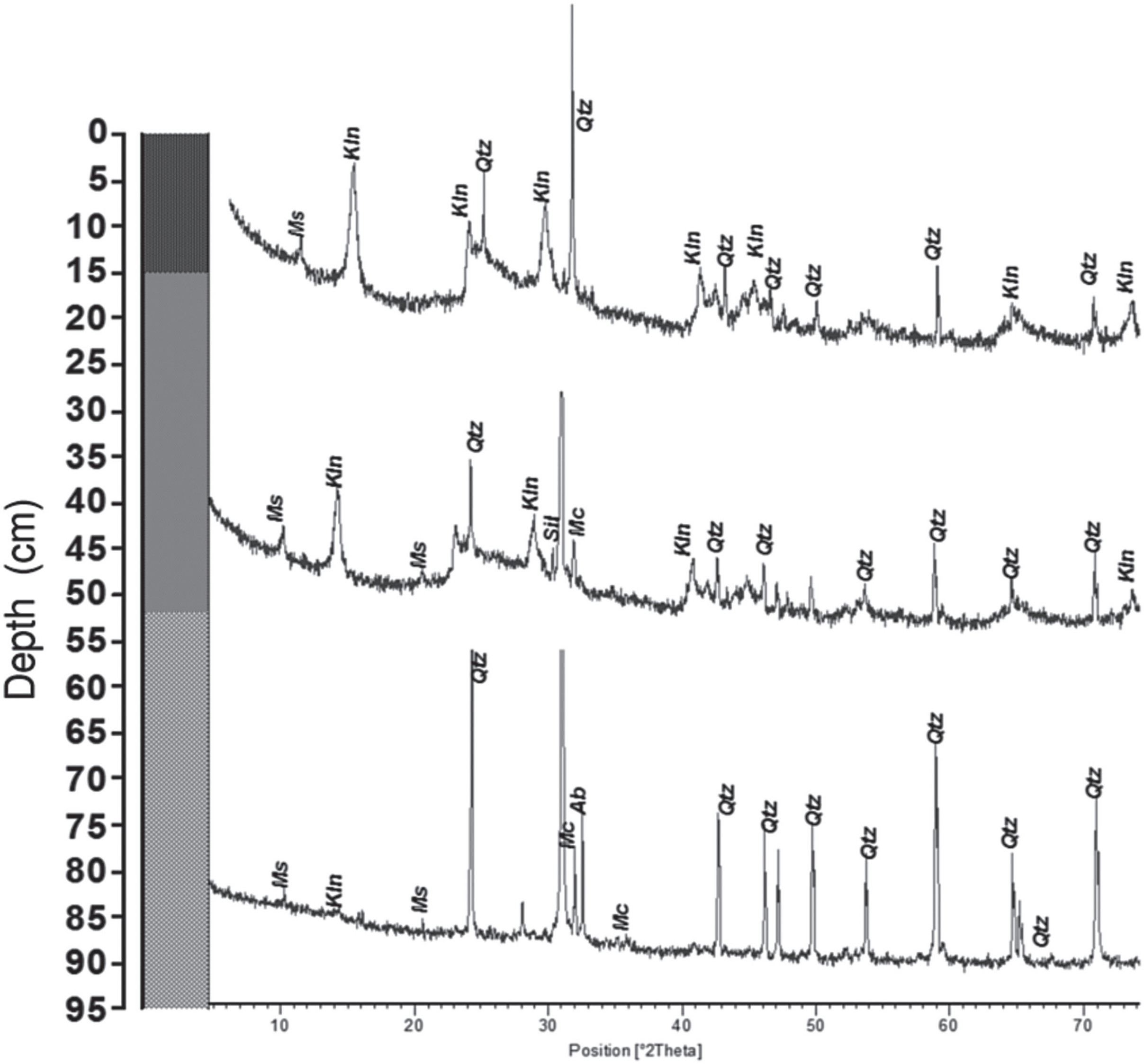

Figure 3 - X-ray diffraction of the AM core that represents patterns of the main minerals found in the core sediments (Qtz- quartz; Kln – kaolinite; Sil – sillimanite; Ms – muscovite; Mc – microcline; Ab – albite).

the core bottom (95 cm) to about 70 cm for these elements. Then, concentrations fluctuate around high counts until around 10 cm core depth, when values start to decrease. This is probably caused by a dilution effect of the increasing organic matter content. The ratio of incoherent to coherent scattering (inc/coh) is commonly regarded as proxy of the organic matter (Guyard et al. 2007), with high inc/coh ratios being indicative of high organic content. The inc/coh ratios show very little variation with a decreasing trend towards the core top until at 10 cm the ratio start to increase indicating a more organic uppermost sediment layer. This likely represents the biogeochemically active zone of the sediment record in which degradation processes of accumulated organic matter take place. The ratio of Fe/Ti can be used as an indicator of redox conditions (e.g. Brunschön et al. 2010), and low Fe/Ti ratios in the lowermost part of core AM indicate more

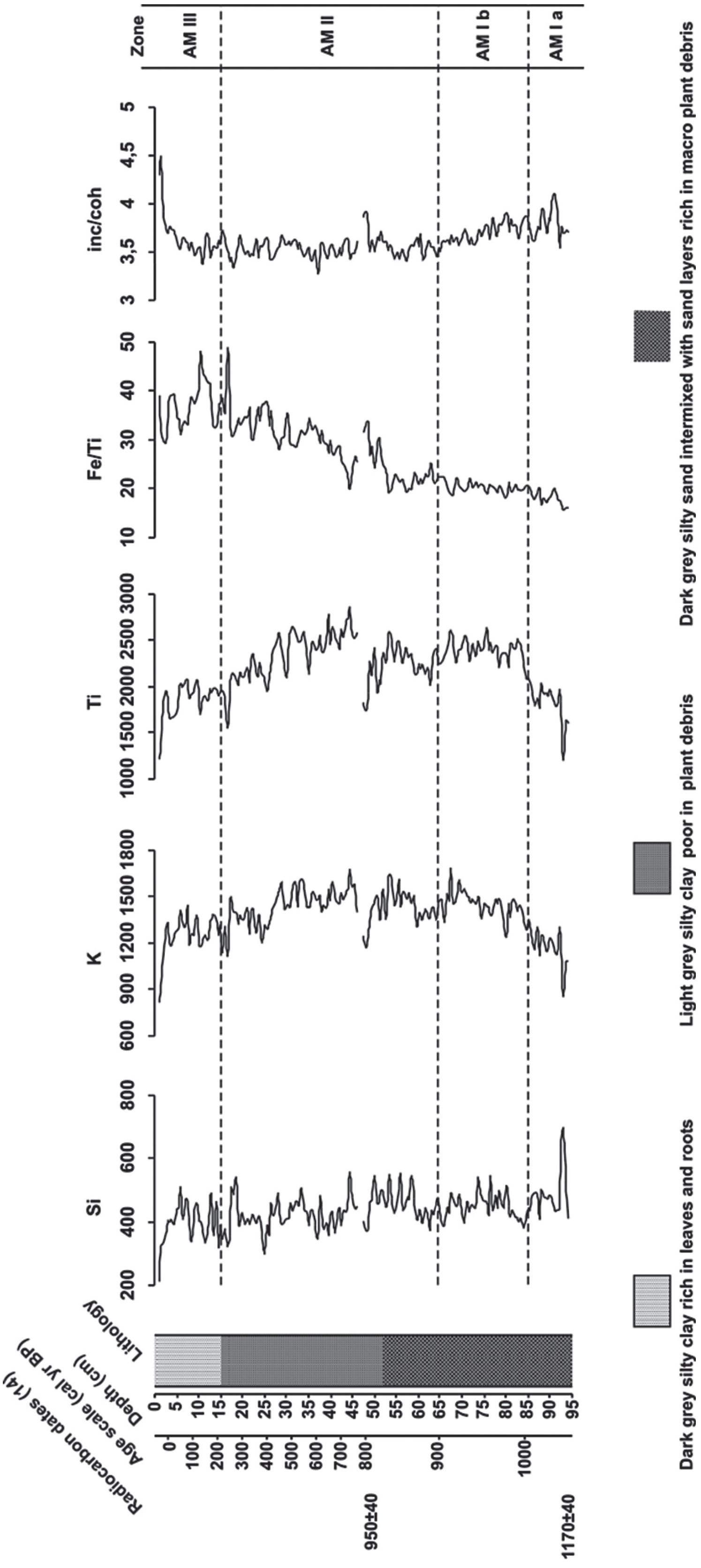

Figure 4 - Diagram showing the element profiles and ratios of the XRF scanning analysis in the AM core, the lithology, ages and the recognized zones.

reducing conditions, being consistent with slight higher organic matter content inferred from the inc/coh ratio. The degradation of organic matter cause anoxic conditions and Fe (III) compounds are reduced to soluble Fe (II) forms leading to a depletion of Fe.

Modern Pollen Rain

Modern pollen assemblages from the surface sediment samples across the three studied vegetation formations (savanna, *Mauritia* and gallery forest and semi-deciduous forest island) are presented in Table III and Figure 5. The modern pollen rain diagram shows the most frequent and important 36 taxa including pollen, spores and algae types which are arranged according to their ecological groups. The compared results of the pollen rain and the modern vegetation data enabled the recognition of important differences among the studied vegetation formations, mainly between savanna and forest systems.

Modern pollen composition of Mauritia palm swamp (sites 1-6)

The proportions of *Maurita flexuosa* pollen (15-37%) are high. Pollen of grassy savanna range between 11 and 26% and consist primarily of Poaceae (2-15%) and Cyperaceae pollen (2-6%).

TABLE III
List of identified pollen in modern pollen rain of the surface sediments samples around AM core site, arranged according to their preferential ecological community.

Savanna	Mauritia swamp forest	Island of forest	Both forests formations
Byrsonima crassifolia	Asteraceae	*Anadenanthera*	*Acalypha*
Cassia	Bignoniaceae I	Arecaceae ret. type	*Alchornea I*
Centrosema	Bignoniaceae II	*Astrocaryum*	*Alchornea II*
Crotalaria	Bombacaceae	*Attalea*	Anacardiaceae
Cuphea	*Caryocar*	*Bauhinia*	Apocynaceae
Curatella americana	*Chamaesyce*	*Casearia sylvestris*	*Cecropia*
Cyperaceae	*Clusia type*	*Coccoloba*	Flacourtiaceae
Desmodium	*Dioclea*	*Cordia*	Malpighiaceae
Drosera	*Echinodorus*	Cucurbitaceae	Melastomataceae
Eriocaulaceae	*Eschweleira*	*Dalechampia*	Moraceae
Eriosema	*Genipa americana*	*Didymopanax*	Myrtaceae
Euphorbiaceae type	*Inga*	Fabaceae I	*Pouteria*
Fabaceae type II	*Isertia*	*Hyeronima*	*Protium*
Fabaceae type III	*Mabea*	*Piper*	Rubiaceae
Galactia	*Macrolobium*	*Tabebuia*	Sapindaceae
Gentianaceae	*Mauritia flexuosa*	*Turbina*	*Swartzia*
Helicteres	Meliaceae	*Vernonia*	**Unknown 1-8**
Hyptis	*Nimphoides*		**Pteridophyta**
Ipomea	*Odontadenia*		Monolete psilate I
Ludwigia	Passifloraceae		Monolete psilate II
Merremia	*Polygonum*		Monolete verrucate
Poaceae	Tiliaceae		Trilete psilate
Polygalaceae	Verbenaceae		Trilete verrucate I
Sida	*Virola*		Trilete verrucate II
Solanum type			*Lycopodium type*
Spermacoce			*Lycopodium cernuum*
Tibouchina type			
Xyris			

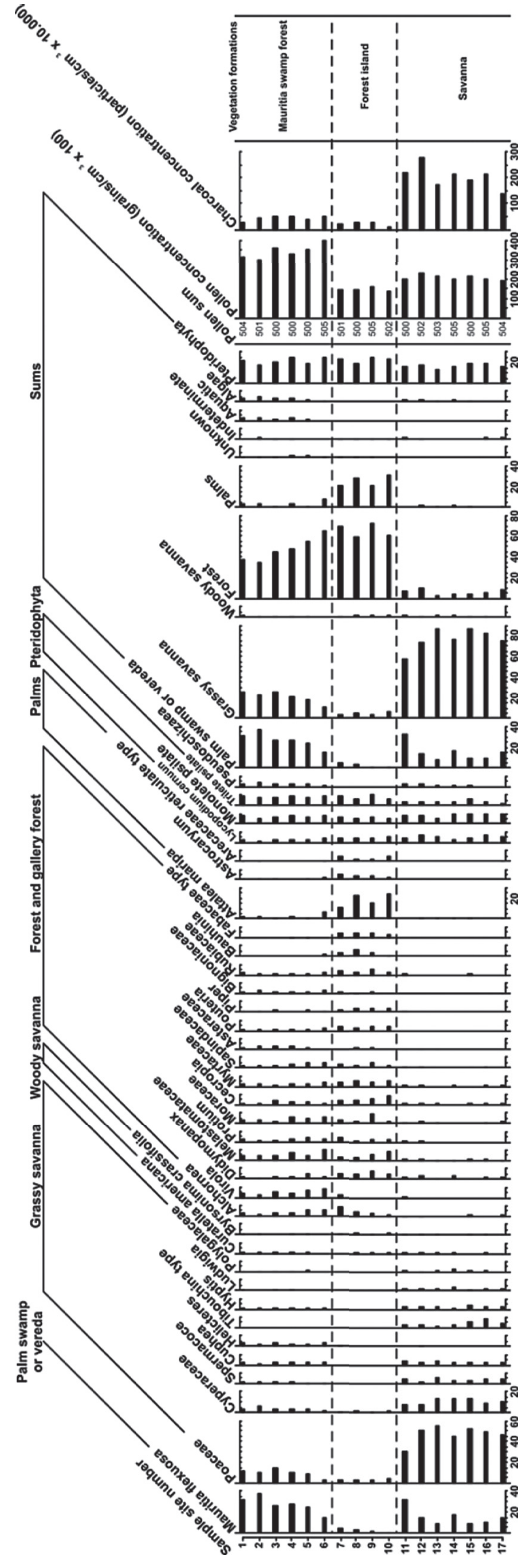

Figure 5 - Diagram showing modern pollen rain percentages of the most frequent taxa as well as the sums, pollen and charcoal concentration.

Helicteres and *Cuphea* pollen values are between 1 and 4% while *Spermacoce* and *Hyptis* pollen occur at levels below 1%. *Curatella americana* coupled with *Byrsonima crassifolia* have low woody savanna values <1%.

Forest taxa vary between 35 and 65%, primarily due to higher pollen frequencies of Melastomataceae (4-9%), *Virola* (2-8%), *Alchornea* (2-6%), Moraceae (2-6%), Sapindaceae (2-5%) and *Didymopanax* (2-4%). *Protium, Cecropia*, Myrtaceae, Asteraceae, Bignoniaceae and *Acalypha* occur at values between 1 and 4%. Palm taxa (1-8%) are dominated by *Attalea* pollen (1-6%). Spores of pteridophyta vary from 17 to 25%. Trilete psilate (7-9%), monolete psilate (5–8%) and *Lycopodium cernuum* (2-3%) are the main spore taxa.

In these sites the pollen concentration (29,700–40,000 grains/cm^3) is higher than in the studied savanna (19,200–23,300 grains/cm^3) and forest sites (13,400–15,700 grains/cm^3). Charcoal concentration (300,800 – 527,300 particles/cm^3) is lower than in the savanna sites (1,3–2,8 million of particles/cm^3) and slightly higher than in the forest island sites (92,200 – 251,600 particles/cm^3).

Modern pollen composition of semi-deciduous forest island (samples 7-10)

The pollen spectrum show high values of forest taxa (60-73%) due to the high representation of *Alchornea* (2-9%), *Cecropia* (4-9%), Melastomataceae (3-9%), Moraceae (2-9%), *Didymopanax* (5-7%), Myrtaceae (3-5%), *Bauhinia* (1-7%) and Rubiaceae (3-5%). Pollen of Sapindaceae, *Piper, Pouteria*, *Protium* and the Fabaceae type occur in values between 2 and 4%. The others forest taxa occur in minor amounts (<1%). The palms group frequency varies from 20 to 31% mainly due to *Attalea* (11–24%), *Astrocaryum* (3-4%) and the Arecaceae reticulate type (2-5%).

Pollen of savanna taxa (3-6%) is poorly represented due to the low values of Poaceae (2-4%) and Cyperaceae (<2%). The *Mauritia flexuosa* pollen (0-4%) is also low in all samples as well as the woody savanna trees (<2%) which are represented only by single pollen grains of *Curatella americana*. Pteridophyta spores (18-25%) are well represented in forest sites, mostly by trilete psilate (6–10%), monolete psilate (5-7%) and *Lycopodium cernuum* (4-5%).

Modern pollen composition of open savanna areas (samples 11-17)

Savanna taxa are predominant in all of the 7 sampled sites with frequencies between 57% and 87%. Pollen of Poaceae (31-55%) and Cyperaceae (8-14%) dominate the pollen spectra of all sites. Other frequent taxa are the *Tibouchina* type (2-8%), *Spermacoce* (2-6%)*, Hyptis* (1-4%)*, Cuphea* (2-3%)*,* Polygalaceae and *Ludwigia* (1-3% each one) that occur with stable proportions. Other savanna types such as Gentianaceae, *Desmodium*, *Drosera, Solanum, Sida* and Eriocaulaceae appear scarcely with singles grains or up to 1%. The pollen of the woody savanna *Curatella americana* and *Byrsonima* trees (all <2%) are few. The *Mauritia flexuosa* pollen vary from 9 to 17% with a highest value of 32% at site 11, where a *vereda* occurs at an initial stage of formation.

Forest taxa represented by Melastomataceae, *Didymopanax*, *Alchornea,* Moraceae and *Cecropia* are less frequent in savanna sites with values from 3 to 10%. *Didymopanax* pollen is the most frequent forest taxon in savanna sites with values of 1 to 3%. The palm group (other than *Mauritia flexuosa*) are poorly represented with values <1%. Spores of pteridophyta (13-19%) mainly monolete psilate (4-9%), trilete psilate (2-5%) and *Lycopodium cernuum* (4-7%) are relatively few in savanna sites.

POLLEN ANALYTICAL RESULTS OF THE THREE CORES

Description of the pollen diagram Amajari (AM)

In total 84 different pollen and spore types were identified in the 20 samples of core AM. The percentage pollen diagram of the most abundant

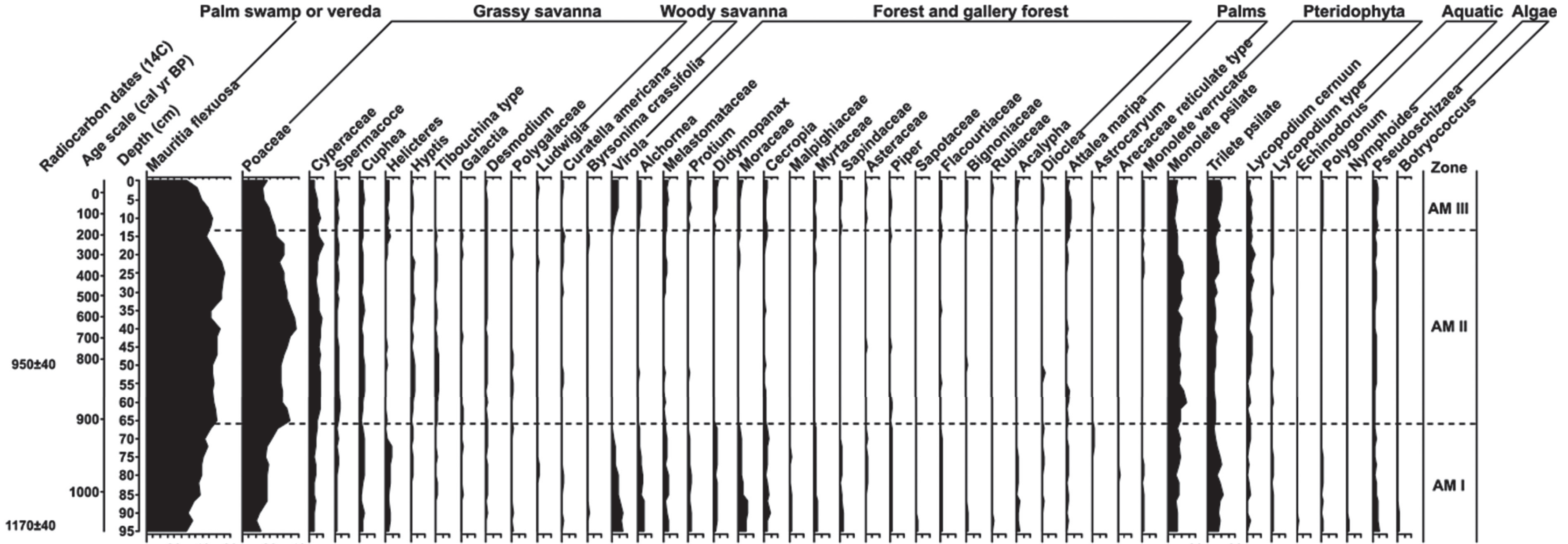

Figure 6 - Pollen percentage diagram of AM core showing the most important taxa grouped into Palm swamp or vereda, Grassy savanna, Woody savanna, Forest and gallery forest, Palms, Pteridophyta, Aquatic and Algae.

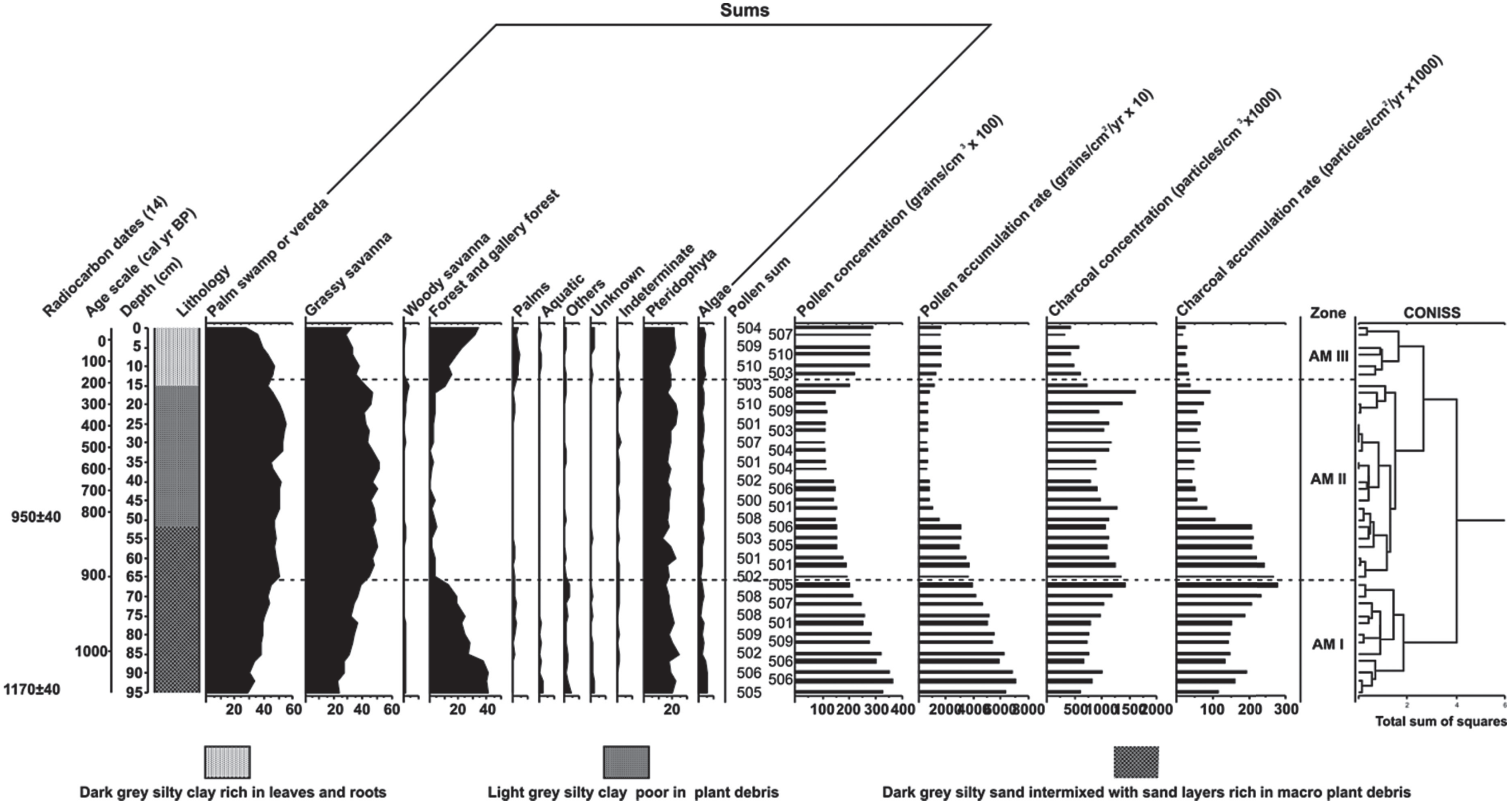

Figure 7 - Summary pollen percentage diagram of the core AM with the AMS radiocarbon dates, age scale, lithology, sums of vegetation groups, pollen and charcoal concentrations as well as pollen and charcoal influx and pollen zones.

taxa is shown in Figure 6. The records of the ecological groups, the pollen sum, as well as pollen and charcoal concentrations and accumulation rates, are illustrated in Figure 7. A cluster analysis based on terrestrial pollen taxa divides the record into three zones AM-I to AM-III (Fig. 7). Pollen concentration values vary from 10,600 to 36,000 grains/cm^3 and pollen influx from 600 to 7000 grains/cm^2/yr along the core, being higher at the base (zone AM-I) than in the following zones towards the top of the core. Charcoal concentration (582.000 –14 million particles/cm^3) and influx (40,000–281,000 particles/cm^2/yr) are very high in the zones AM-I and in the beginning of the zone AM-II decreasing in the end of this zone until zone AM-III.

Zone AM-I (95–67 cm; ca. 1050–900 cal yr BP) is marked by a high pollen representation (13–41%) of forest taxa such as *Virola* (0–7%), Moraceae (1–6%), Melastomataceae *(*2–4%), *Alchornea* (1–5%) and *Cecropia* (1–4%). Other forest taxa such as *Protium, Didymopanax, Acalypha*, Myrtaceae, Sapindaceae, Asteraceae and *Piper* have lower values (<2% each). Pollen of *Mauritia flexuosa* increases from 29% in the lower part of the zone, to 45% in the upper part of the zone. Grassy savanna pollen (22–38%) are well represented, especially Poaceae (10–25%) and Cyperaceae (3–5%). Pollen of *Helicteres* (1–4%), *Spermacoce* (1–2%), *Cuphea* (1–3%) and *Hyptis* (0–2%) occur in minor proportions. Percentages of the woody savanna group are low due to the low frequency of *Curatella americana* and *Byrsonima crassifolia* pollen (all 1-2%). Aquatic taxa (0–3%) are represented by small amounts of *Polygonum* and *Nymphoides.* Th*e* algae group (1–5%) is composed mainly by *Pseudoschizaea* (1–4%) and single colonies of *Botryococcus.* Pteridophyta values (14–23%) are high in this zone due to monolete psilate *(*5–9%), trilete psilate (5–10%) and *Lycopodium cernuum* spores (1–3%).

Zone AM-II (67–15 cm; ca. 900–210 cal yr BP) is characterized by high pollen frequency (42–55%) of *Mauritia flexuosa* as well as grassy savanna taxa (41-51%), primarily Poaceae (24-38%) and Cyperaceae (4–10%). Other taxa such as *Spermacoce* (1-4%)*, Cuphea* (1-3%), *Hyptis* (0-3%) and *Helicteres* (0-3%) have lower representations. Pollen of forest taxa are strongly reduced (1% or lower), but show an increase (10%) at the top of the zone. Other forest pollen taxa with low amounts include *Virola*, *Alchornea*, Melastomataceae, Moraceae, *Didymopanax, Cecropia*, *Protium* and Sapindaceae. Woody savanna pollen taxa (<2%) show low values being nearly absent from most of this zone. Palm taxa are rare as well as are aquatic pollen. Spores of pteridophyta vary between 13 and 23%. Monolete psilate (7–13%), trilete psilate (4–8%) and *Lycopodium cernuum* (1–6%) are still the most important taxa.

In zone AM-III (15–0 cm; ca. 210 cal yr BP to modern times) the proportions of *Mauritia flexuosa* pollen (28–47%) are slightly lower than in the previous zone with a decreasing trend towards the top of the zone. Poaceae pollen (15–22%) decrease at the top of the core, while Cyperaceae pollen (3-7%) remain relatively stable. Pollen of the grassy savanna group corresponds to values between 29 and 38%. Values of *Spermacoce*, *Hyptis, Helicteres* and *Cuphea* pollen are low (<3%). Similar to the previous zone, woody savanna taxa are rare (<1%). Forest taxa increase markedly from 12-15% to the highest value of 33% at the top of the core, reflecting the increasing frequencies of *Virola* (1-4%) and Melastomataceae (2-3%) among other. Pollen values of *Alchornea, Didymopanax*, *Cecropia,* Moraceae are between 1 and 3%, Myrtaceae and Sapindaceae are <2 %. Palm taxa (2-4%) are represented by *Attalea* pollen in low amounts (2-3%). Spores of pteridophyta vary from 21 to 23%. Trilete psilate (7-10%), monolete psilate (4–6%) and *Lycopodium cernuum* (2-4%) are the main spore taxa.

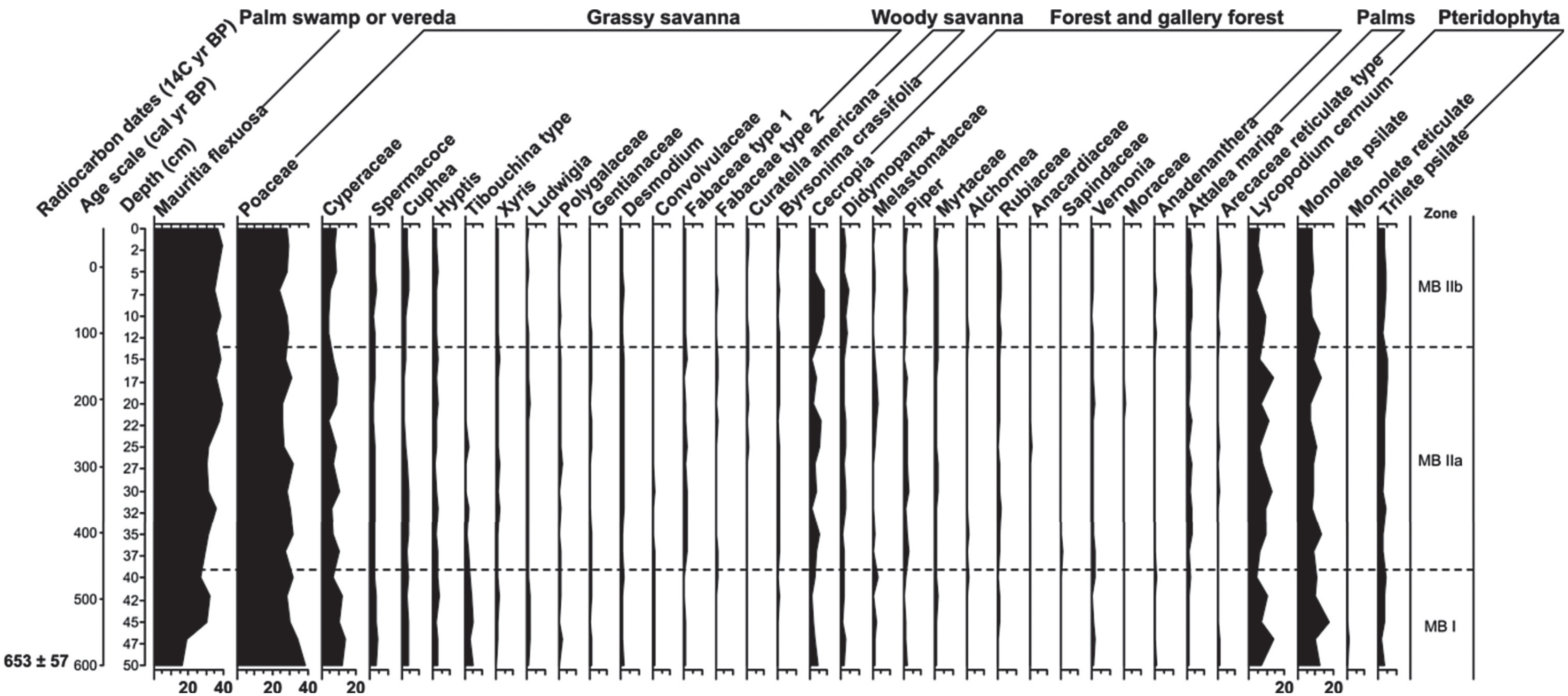

Figure 8 - Pollen percentage diagram of MB core showing the most important taxa grouped into Palm swamp or vereda, Grassy savanna, Woody savanna, Forest and gallery forest, Palms and Pteridophyta.

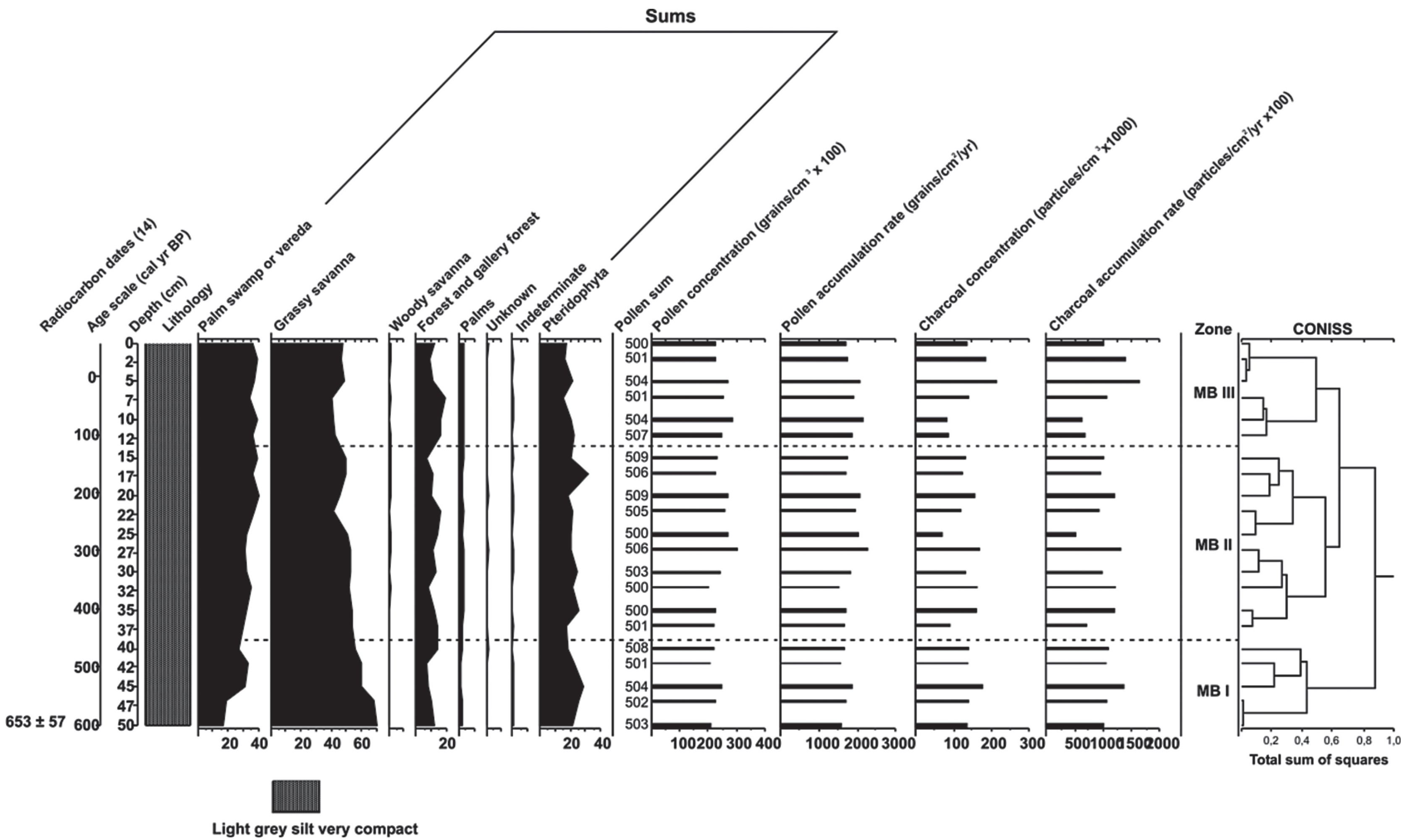

Figure 9 - Summary pollen percentage diagram of the core MB with the AMS radiocarbon dates, age scale, lithology, sums of vegetation groups, pollen and charcoal concentrations as well as pollen and charcoal influx and pollen zones.

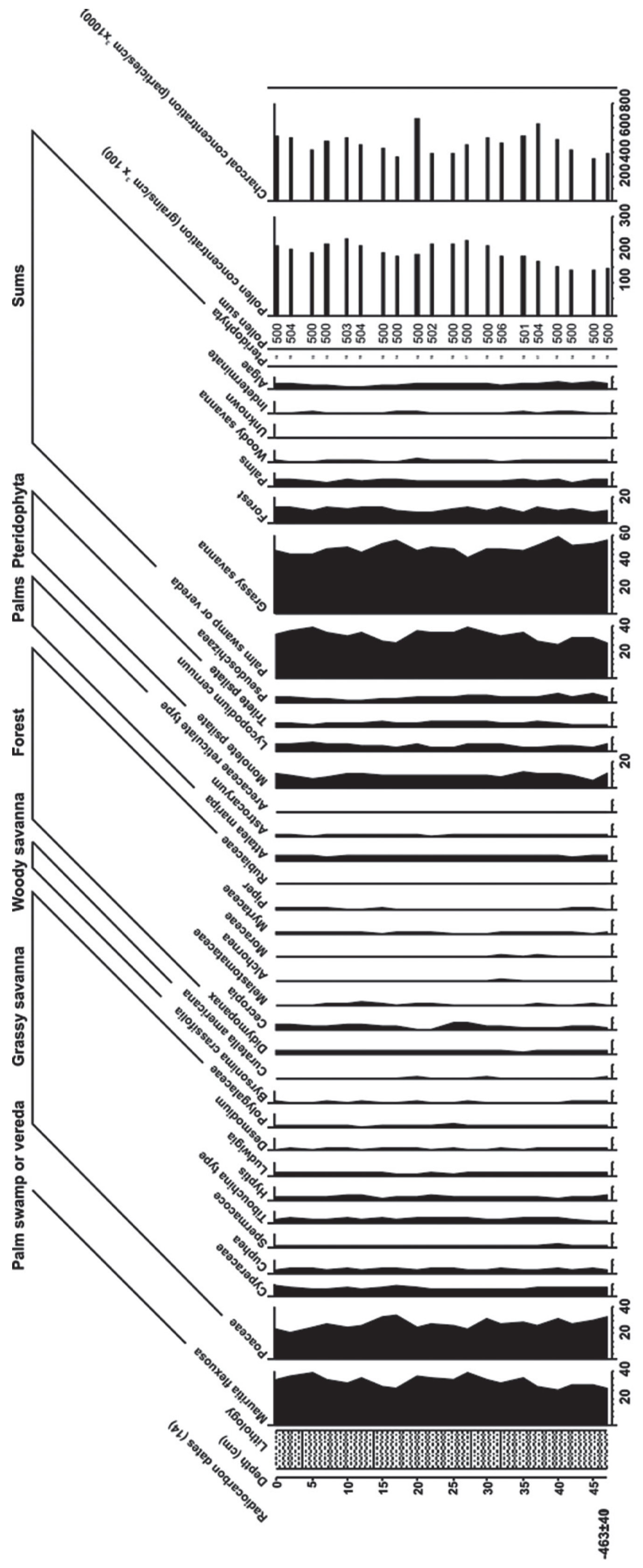

Figure 10 - Pollen percentage and summary diagram of the RU core showing the AMS radiocarbon dates, the lithology, selected pollen and spore taxa grouped into Palm swamp or vereda, Grassy savanna, Woody savanna, Forest, Palms, Pteridophyta and Sums, in additional to pollen and charcoal concentrations.

Description of the pollen diagram Maloca do Boqueirão (MB)

A total of 21 samples were analyzed in core MB. The most abundant 34 taxa from a total of 53 pollen and spore types are shown in the percentage diagram (Fig. 8). Identified pollen and spores grouped into different vegetation types are illustrated by a summary percentage diagram (Fig. 9). Two zones are distinguished by cluster analysis (MB-I and MB-IIa and MB-IIb). Pollen concentration (20,100–30,000 grains/ cm^3) and influx (1500–2300 grains/cm^2/yr) remain relatively stable along the entire core. The values of charcoal concentration (819,000–2,1 million particles/cm^3) and influx (51,000–163,300 particles/cm^2/yr) are high, with a slight increase at the top of the core in zone MB-IIb (Fig. 9).

Zone MB-I (50–40 cm, ca. 600–470 cal yr BP) is characterized by a high proportion (55–70%) of grassy savanna taxa with the lowest values at the uppermost part of the zone due to a decrease of Poaceae (31–38%) and Cyperaceae (7–14%) pollen. Other taxa are *Spermacoce* (3–4%), *Cuphea* (3–4%), the *Tibouchina* type (3–5%), *Hyptis* (2–3%), *Xyris* and *Ludwigia* (0-2%) recorded in stable proportions. *Mauritia flexuosa* pollen start with 16% and increase to 32% at the top of this zone. Woody savanna taxa (<1%) are poorly represented due to the rare occurrence of *Curatella americana,* and *Byrsonima crassifolia*. Forest taxa (6–13%) consist mostly of pollen of *Cecropia* (1–4%), *Didymopanax* (1–2%), *Piper* (0–2%) and Melastomataceae (1–3%). The group of palms have stable values around 1-2% due to low amounts of *Attalea* pollen (1–2%) and the Arecaceae reticulate type (<1%). Pteridophyta spores vary between 18 and 28%; the most important representatives are monolete psilate (9–17%), *Lycopodium cernuum* (4–13%) and trilete psilate spores (2–4%).

Zone MB-IIa (40–15 cm, ca. 470–140 cal yr BP) shows high and stable proportions (42–53%) of savanna taxa indicated by constant values of Poaceae (25–32%) and Cyperaceae pollen (4–10%). *Spermacoce* (1–2%), *Cuphea* (1–4%), *Hyptis* (1–3%), the *Tibouchina* type (0–3%), *Xyris* and *Ludwigia* (<1%) decrease in comparison to the previous zone. The *Mauritia flexuosa* values increase from 30% at the lower part to a maximum of 39% at the upper part of this zone. Forest taxa vary from 6 to 16% mainly by *Cecropia* (1–6%), *Didymopanax* (1–3%), *Piper* (1–2%) and Melastomataceae pollen (0–3%). Palm taxa (2-4%) show slightly higher values in comparison to the previous zone. Pteridophyta spores fluctuate between 17 and 32% within this subzone. In zone MB-IIb (15–0 cm, ca. 140 cal yr BP to present-day) the savanna proportions occur at levels of 40 to 48% dominated primarily by Poaceae (24–29%) and Cyperaceae (5–8%). The other more important savanna taxa remain at the same levels as in those the previous subzone. Forest taxa reach a maximum value of 19% due to higher pollen frequencies of *Cecropia* (3–8%) and *Didymopanax* (3–8%). The other forest taxa (e.g. Melastomataceae, Myrtaceae, *Piper* and *Alchornea*) maintain the same levels recorded as before. The same is found for palm taxa (3-4%) dominated mostly by *Attalea* (2-3%) pollen. Pteridophyta spores decrease and have values between 16 and 22%.

Description of the pollen diagram Uraricoera river (RU)

The pollen record of the RU site in general shows few changes along the core (Fig. 10). The pollen concentration also displays few variations (13,700-23,350 grains/cm^3) being somewhat lower at the bottom of the core. Charcoal particle concentrations are lower (340-660,000 particles/cm^3) than in the other studied cores.

The entire pollen spectrum (47–0 cm, 10 subsamples) that represents deposition of modern times is characterized by high percentages of *Mauritia flexuosa* pollen (25–38%) as well as savanna taxa such as Poaceae (20–34%), Cyperaceae (4–8%), *Tibouchina* type (2–5%), *Cuphea, Hyptis* and *Ludwigia* (1–3% each ones). Woody savanna taxa (0–2%) are poorly represented due to low values of *Curatella americana* and *Byrsonima crassifolia*. The forest pollen (8-13%) values are stable, represented especially by *Cecropia* (1–5%), *Didymopanax* (1–4%) and Melastomataceae (0–2%). *Alchornea*, Moraceae, Myrtaceae and *Piper* have lower values (<1%). The palm taxa vary between 3 and 5% mostly due to *Attalea* pollen (2–4%). Pteridophyta spores (10–19%) values are stable represented by monolete psilate (6–11%), *Lycopodium cernuum* (2–6%) and trilete psilate (1–4%).

DISCUSSION

Modern Pollen Rain – Vegetation Relationship

Regarding the savanna system, Poaceae and Cyperaceae are the most abundant taxa occurring in savanna vegetation and also in the pollen rain data. Cyperaceae are normally regarded as species of wet or aquatic environments, but they occur throughout the Roraima savanna occupying both dry and wet sites. According to Miranda (1998), the Cyperaceae family is one of the most important components of this open vegetation whose importance is also reflected in the pollen rain.

A high number of different species growing in savanna are represented at least by single pollen grains in the surface samples. However, some taxa show a closer similarity, for example, *Tibouchina*. This shrub with high abundance across the savanna marshlands can be distinguished from the other Melastomataceae pollen by its bigger size. *Spermacoce* pollen probably represents those taxa listed as *Borreria* in the floristic inventory. *Ludwigia* is also a very common shrub occurring along the savanna marshes. The absence of Asteraceae in the savanna pollen spectrum reflects its rarity in this vegetation type (Wijmstra and Van der Hammen 1966).

It is interesting to note that the most frequent pollen grains found in the sediments from savanna sites are characteristic of marsh vegetation (e.g. *Spermacoce, Tibouchina, Cuphea, Hyptis, Ludwigia,* Polygalaceae and *Xyris*). Species of Poaceae and Cyperaceae also occur in these wet places, but they are palynologically not distinguishable from other types. *Curatella americana* and *Byrsonima* are the main components of woody savanna cover, but are less important in the pollen rain (<2%).

With regard to the forest sites, a distinction between the pollen signal of *Mauritia* swamp forest and semi-deciduous forest island is difficult due to the occurrence of several taxa in both forest types, mainly *Alchornea*, Moraceae, Melastomataceae, Myrtaceae, Sapindaceae and Rubiaceae. However, some differences can be observed, e.g. the occurrence of *Mauritia flexuosa*, *Virola*, Asteraceae and Bignoniaceae in the *Mauritia* swamp forest sites and their almost total absence in the semi-deciduous forest samples. Many other less common taxa also help to separate the formations from each other. For example, the occurrence of the *Macrolobium* type, *Genipa americana, Inga* and some taxa belonging to the family Euphorbiaceae e.g. *Sebastiania, Chamaesyce* (not shown in diagram) that are represented by values up to 1% in the *Mauritia* swamp forest.

On the other hand, some taxa are well represented in the semi-deciduous forest and rarer or absent in the *Mauritia* swamp forest such as *Bauhinia*, the Fabaceae type and mostly the palms of *Attalea*, *Astrocaryum* and the Arecaceae reticulate type (probably *Pyrenoglyphis*, an abundant palm tree along the forest island). The proportions of *Cecropia, Piper* and *Didymopanax* in the forest island sites are higher than in the *Mauritia* swamp forest. The constant presence of *Didymopanax* along all the studied vegetation formations is surprising, as this genus is not anemophilous. *Didymopanax* is a well-known shrub growing in savanna sites e.g. *Llanos Orientales* from Colombia (Behling and Hooghiemstra 2000, Berrio et al. 2002). However, in the studied region, it is probable that

Didymopanax occurs as a shrub growing into the forest, as indicated by its highest pollen frequency inside the forest samples. Since *Didymopanax* is not wind-pollinated and has hermaphrodite flowers, its representation in the pollen rain of all studied samples can be attributed to its "messy pollination syndrome" whereby its very open flower structure with large number of exposed anthers results in easily dispersed pollen grains (Gosling et al. 2005).

In general the pollen rain signatures of both forests reflect, in part the unique floristic elements of the vegetation types, and in part the shared taxa belonging to the families Moraceae, Sapotaceae, Myrtaceae, Rubiaceae, Euphorbiaceae, Flacourtiaceae, Malpighiaceae, Fabaceae and many others. Although Melastomataceae and Combretaceae pollen grains cannot be differentiated one from another, we assume that this group represents Melastomataceae, especially *Miconia* and *Clidemia*, inferred by their abundance in the *Mauritia* swamp forest as well as in the semi-deciduous forest and more rarely in the savanna areas. As for Combretaceae, no occurrence was found in the modern vegetation.

Most of the taxa listed in the floristic inventories are also found in the modern pollen samples, but several families that occur abundantly in the forests and also in the savanna vegetation (such as Annonaceae, Lauraceae, Chrysobalanaceae, Monimiaceae, Proteaceae, Olacaceae, Simaroubaceae) are missing in the pollen assemblages. Specific particularities in the pollen production, dispersal power and preservation conditions could be responsible for such anomalies (Behling and Negrelle 2006). For example, *Xylopia aromatica* and others Annonaceae species are well represented in the savanna vegetation, but were not found in the pollen rain samples, probably because they have very fragile pollen grains (Salgado-Labouriau 1973).

The modern pollen spectra from the Roraima savanna, *Mauritia* swamp forest and semi-deciduous forest island ecosystems, are clearly distinct from each other. Few pollen grains are found outside their producing community. While the savanna pollen spectrum is easily differentiated from those from the forests, the distinction between *Mauritia* swamp forest and semi-deciduous forest ecosystems is more difficult, because several taxa are common to both ecosystems. However, the exclusive or higher occurrence of some taxa such as *Mauritia, Virola* and *Macrolobium* (all in *Mauritia* swamp forest) and *Attalea* and the the Arecaceae reticulate type (in the forest) in each environment enable the distinction between them. Thus, the modern pollen rain data allowed the reconstruction of vegetation changes for the last recorded 1050 cal yr BP.

ENVIRONMENTAL CHANGES: VEGETATION, CLIMATE AND FIRE DYNAMICS

The pollen record of the Uraricoera River (RU) core probably only represents recent pollen rain from this site. The vegetation cover at RU is reflected in the pollen diagram through high percentages of *Mauritia flexuosa* and taxa of wet soils, especially *Tibouchina, Spermacoce, Hyptis, Cuphea* and *Ludwigia.* This palm swamp is surrounded by grassy savanna with abundant Poaceae and Cyperaceae scattered by shrubs of *Curatella americana* and *Bysonima crassifolia* while the secondary forest rich in palms (*Attalea, Astrocaryum* and *Pyrenoglyphis*) occurs in adjacent places. The high charcoal concentration in the RU sediment deposits, demonstrate that fires were frequent at the site.

The Amajari (AM) records span back to about 1050 cal yr BP. At that time a *Mauritia*-dominated palm swamp started to form with an accumulation of pollen-rich organic material, indicating a higher water table. The lowermost part at 90-95 cm core depth shows relatively low counts of K and Ti suggesting less minerogenic input, probably indicating a spring-fed *Mauritia* swamp. Upwards, the values of K and Ti slightly increase, indicating more contribution of the run off from the surrounding soils into the new-formed palm swamp, becoming relatively stable in the following zone AM-II. The intercalation of fine sandy layers in the silty sand sediments is evidence of an alternation between fluviatile and stagnant conditions or, more likely, local soil erosion events triggered by torrents during episodic strong storms which are typical of the seasonal wet climate, similar to the climatic conditions of today. Despite coarser sediment intermixing with the finer sediment matrix (95 – 65 cm) in the zone AM-I, pollen preservation is very good and also the concentration and influx of pollen are higher than in the following periods. A hydromorphic environment with anoxic conditions as supported by a lower Fe/Ti ratio might have contributed to preserve the pollen grains.

The presence of *Mauritia* pollen in the sediments is a reliable indicator of warm tropical lowland environments flooded by fresh waters (Rull 1998, Marchant et al. 2002). The algae remains of *Botryococcus* and *Pseudoschizaea* and some aquatic taxa such as *Nymphoides, Echinodorus* and *Polygonum* suggest a shallow and temporary stagnant water body.

The pollen assemblages suggest that a forest, probably a gallery forest, was present as indicated by the occurrence of *Virola, Alchornea*, Melastomataceae, Moraceae, *Protium* and Sapindaceae. *Helicteres* and *Cuphea* occur in high frequencies and are evidence of wet soils. Asteraceae (probably lianas) and *Cecropia* trees were common at the borders of this forest. The high percentages of *Didymopanax* pollen suggest that a semi-deciduous forest patch (secondary forest) was in the vicinity, also supported by many taxa mentioned for the gallery forest (except *Virola*, *Mauritia flexuosa*) as recorded within the modern pollen spectra. It is probable that a grass-dominated savanna occurred in the neighborhood of the AM site.

The results indicate moist conditions during this whole period, lasting from 1050 until 900 cal yr BP (zone AM-I). The lower concentration and influx of charcoal particles in the sediment suggest that fires were less frequent, but increased at the end of this period. However, it is possible that fires occurred only in the savanna area and could not penetrate into the forest area. This assumption is based on values of modern charcoal particle concentrations around the coring AM site, which were higher in the savanna sites than in the forest sites.

The period from 900 to 210 cal yr BP (zone AM-II) has lower pollen concentration and influx compared to the previous period. Hence, the low pollen influx probably indicates a reduction in vegetation cover. Indeed, the forest cover decreased in this period as indicated by reduced pollen of *Virola*, Melastomataceae, *Protium*, Moraceae, *Acalypha* and of all the other forest taxa including palms except *Mauritia*. The high concentration of carbonized particles shows that fires played an important role during this period. Presumably these fires reduced the forest cover as documented in other places in the Amazon region, e.g. the high Rio Negro basin where frequent fires caused the destruction of several forest types during the mid- and late Holocene (Santos et al. 2000, Sanford et al. 1985). The marked expansion of savanna grasses during this period might have been favored by increasing fires. *Mauritia flexuosa* palms also increased, forming a denser corridor than before. The disappearing of *Botryococcus* and aquatic taxa such as *Nymphoides* and *Polygonum* reflect a lower water level. On the other hand, *Pseudoschizaea* remains constant, suggesting that humid conditions still occurred at least seasonally. The presence of *Mauritia flexuosa* palms is coupled to typical savanna swamp taxa such as *Tibouchina, Cuphea* and *Hyptis* and suggests that a swamp existed locally at this site during this period. The conditions of sedimentation change at the 52 cm depth interval and the previously sandy material is now replaced by finer sediments and it is possible that the environment switched to lower-energy conditions. Perhaps the basin was isolated from the regional drainage system, caused by less strong rainfall events.

At the study site Maloca do Boqueirão (MB) the regional climatic situation was favorable to form a *Mauritia flexuosa* palm swamp around 600 cal yr BP. From this period until 470 cal yr BP (zone MB-I) the MB site supported a swamp, inferred by pollen of *Spermacoce*, *Cuphea*, the *Tibouchina* type, *Hyptis*, *Xyris* and *Ludwigia* and an increasing population of *Mauritia flexuosa* palms. This palm swamp was surrounded by a treeless savanna dominated by Poaceae and Cyperaceae. Trees of *Curatella americana* and *Byrsonima crassifolia* were always rare, probably affected by frequent fires. A secondary forest developed relatively close to the area indicated by pollen representation of pioneer taxa such as *Cecropia*, *Didymopanax*, *Piper* and by palms like *Attalea* and other Arecaceae (reticulate type, probably *Pyrenoglyphis*) which are very common in disturbed settings. The fire events were apparently very frequent with small variations throughout the past 600 years. It is possible that these fires hampered the expansion of forest patches and the establishment of gallery trees (*Virola,* for example) as well as the successful development of shrubs or trees of the families Melastomataceae, Myrtaceae and Rubiaceae and other along the palm swamp as it is normally expected under wet climatic conditions. This environmental situation is marked by a dominant savanna, rich in Poaceae and Cyperaceae, with a dense *Mauritia flexuosa* palm swamp and surrounded by small patches of forest which did not change until present-day. Fires are still frequent in this area.

At the site AM, from the 210 cal yr BP until modern times (zone AM-III) the sediments became slightly darker and rich in plant debris in comparison to the previous periods in response to the re-establishment of a perennial swamp with forest trees growing close to a relatively small open water body. In recent times, the water level of the palm swamp apparently increased allowing the reappearance of aquatic plants and algae.

The gallery forest slightly expanded forming the current *Mauritia* palm swamp. The moisture-requiring tree *Virola* increased in abundance, as well as other forest taxa such as *Alchornea,* Moraceae, Bignoniaceae and Melastomataceae. The increase of *Didymopanax*, and palms such as *Attalea* and other Arecaceae (reticulate type) suggest that a secondary forest occurred close to AM during this period, as observed today. This modern forest island may have resulted from an enlargement of the *Mauritia* swamp forest towards drier soils of nearby slopes forming a patch or island like many other commonly found throughout the savanna region. Such assumption is based on the similar floristic composition (except for moist taxa such as *Mauritia* and *Virola*)*,* and geomorphological observations in the region. The expansion of these forests could be interpreted as a signal of gradually moister conditions during the last two hundred years or alternatively as a result of the decreasing fire frequency in the region, inferred by the lowest charcoal particles concentration and influx in the uppermost samples at AM.

The fire decline after 500 cal yr BP might be the main reason for the expansion of secondary forests and forest recovery, as has been previously documented in several other places of tropical South America such as Ecuador (Niemann and Behling 2008), Colombia (Wille et al. 2000), Panama (Bush and Colinvaux 1994, Bush et al. 1992) and in southern Brazil (Behling et al. 2004, Jeske-Pieruschka et al. 2010). The reduction of fires, which are assumed to be of anthropogenic origin, is possibly related to the collapse of the indigenous population after the arrival of European settlers (Nevle and Bird 2008, Wille et al. 2000). According to Denevan (1992) the introduction of Old World diseases by the Conquistadors contributed to such a depopulation.

In the Roraima region, the earliest human occupation was dated to around 4000 cal yr BP, and the Ameridians were hunters and farmers using fire for hunting and the clearing of land (Ribeiro 1997). European settlers arrived in this region after

1750 AD (200 cal yr BP). The first attempts of colonization process were based on enslavement of the indigenous people which resulted in revolts, fights and their escapes towards more inaccessible mountain refuges. Hence, a decrease of these populations and subsequently an anthropogenic fire decline is likely.

Nevertheless, fires still occur frequently today as indicated by charcoal concentration of modern and fossil sediments, but with some variability from one place to another. For instance, at MB and AM sites the fires are more frequent than at RU site.

These differences result from modern land use. The AM site is located close to active cattle ranches and the MB site belongs to indigenous land where agricultural activities using simple techniques are widely practiced. In contrast, the RU site is more distant from these human inhabited places. Similarly, in a study about modern burning in the Roraima savanna, Barbosa and Fearnside (2005) demonstrated that the greatest occurrences of fires are more concentrated close to the headquarters of the cattle ranches and to indigenous villages, than to other areas. According to the authors, fires in the savannas of Roraima are typically anthropogenic, because lightning (potential cause of natural fires) in Amazonia is almost always accompanied by rain, reducing the chance of igniting a natural fire. As no considerable climate change with prolonged dry periods is suggested by our analyses, we assume the higher fire frequency was caused by humans rather than by lightning. Although the decline of indigenous population might have caused a decrease of fire during the past centuries, modern human activities such as cattle farming and agriculture are still responsible for fire in modern times.

The comparison of charcoal concentrations of surface sediments from savanna and forested sites showed that fire was more frequent at savanna sites than in forests (especially in the forest island). Apparently the forest cover, even as narrow strips of gallery forest or small patches of forest, acts as an effective buffer blocking the entry of both fire and airborne charred particles into these environments.

In general our findings suggest that the recorded environmental changes from AM and MB cores are mostly related to vegetation changes which were driven much more by fire dynamics than by climate change. At both sites, the records suggest a stable wet climate as indicated by *Mauritia flexuosa* associated with pteridophyta and taxa characteristic of wetlands. In this context, a study previously carried out in Roraima savanna-forest region showed that climate was favorable to expansion of forest, especially gallery forest since 1550 years. However, several phases of forest retreat were verified while the *Mauritia* palm swamps increased considerably (Da Silva Meneses et al. 2013). Hence, the authors also concluded that the fire was the main controlling factor of the vegetation dynamic since that climate was wet during the entire recorded period, as indicated by enlargement of *Mauritia* palm swamps.

The wet climatic conditions have been favorable for the establishment and development *of Mauritia* palm swamps during all recorded times until the present-day. A huge number of corridors of *Mauritia* palms are found across the savanna, occupying innumerable swamps formed by high ground water levels on poorly drained soils. According to Kahn (1987), the abundance of *Mauritia* is the result of an increase in precipitation. In this respect, the substantial increase of mainly *Mauritia* palms since about 4000 cal yr BP is verified at Laguna Loma Linda (Behling and Hooghiemstra 2000), Laguna Las Margaritas (Wille et al. 2003) and in many other studied sites in the Llanos Orientales. This has been assumed as an indication of wetter conditions caused by enhanced precipitation in the region (Marchant et al. 2001, 2002, Berrio et al. 2002). On the other hand, the increase of *Mauritia* palms during the late Holocene is interpreted as enhanced human activity by use of fires under wet climatic conditions (Behling and Hooghiemstra 1998, 1999, 2000, Montoya and Rull 2011, Montoya et al. 2011).

In the Roraima region, human impacts are reflected in a diminished species richness of forest islands due to past and modern human activities. The abundance of *Didymopanax* growing in forests with an open canopy is likely evidence of the human impact on the vegetation by slash and burn activities (Behling and Costa 2000, Marchant et al. 2002), even at places where agricultural activities are rare or absent. The constant presence of the short-lived pioneer *Cecropia* reinforces the disturbed nature of this forest as well as the large number of palms (*Attalea* and other species). Fire impacts are responsible for the impoverishment of the forests. Therefore, fire is thought to be one of the main reasons for maintaining the sharp boundaries between the forests and savanna. Pioneer tree species growing into the savanna probably do not tolerate fire (e.g. *Bowdichia virgilioides*), and consequently, frequent fires will hamper forest expansion. Additionally, the occurrence of hydromorphic, sandy soils around existing forest areas (including the margins of the palm swamps) could be acting as a further barrier for the establishment of forest trees species.

CONCLUSIONS

The integrated pollen and sedimentological records show that wet conditions prevailed during the last 1050 years at sites Amajari (AM) and Maloca do Boqueirão (MB). The persistent *Mauritia flexuosa* palm swamps, suggest wet soils promoted by high precipitation rates with a probable short dry season (4 months on average), similar to the present-day situation. Despite these moisture conditions, fires of probably anthropogenic origin were always frequent and markedly influenced the vegetation development of this savanna-forest mosaic in the northern portion of the Roraima region. These fires probably hampered a wider forest expansion and together with cattle farming, which were introduced at around 170 cal yr BP (1780 AD) in the region, also maintain the current sharp boundaries between savanna and forests areas. The occurrence of nutrient-poor hydromorphic soils in the adjacent areas probably also hinders the establishment of forest trees and thus forest expansion. Our results are in accordance with the sedimentological studies carried out in Lake Caracarana, which show a wetter climate developed in the area over the last 2000 years (Simões Filho 2000). The forest expansion with installation of *Mauritia* palm swamp was observed by pollen data for other two sites previously studied in this savanna-forest region and reflects the wetter climatic conditions during the past 1550 years (Da Silva Meneses et al. 2013). Trends of a late Holocene forest expansion were also inferred by isotopic data from a site close to Boa Vista city (Desjardins et al. 1996).

The new results provided by this study represent a first approach to gain insight into the environmental factors that are responsible for the savanna-forest mosaic in the state of Roraima. Due to the diversity of environments found across the savanna-forest boundary, more investigations in the form of multi-proxy studies are necessary to distinguish between local effects and regional trends related to human impact and climatic changes.

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RESUMO

As mudanças ambientais e a dinâmica do mosaico savana-floresta durante os últimos 1050 anos foram reconstituídos através de análises palinológicas, de partículas carbonizadas, datação radiocarbônica, mineralógicas e geoquímicas de testemunhos de sedimentos amostrados a partir de três diferentes veredas de *Mauritia flexuosa*, na porção mais setentrional da região amazônica brasileira (norte do estado de Roraima). Estudos da relação entre a chuva polínica atual e a vegetação regional fornecem informações complementares para a interpretação dos registros polínicos fósseis. Os resultados das análises das assembleias de pólen fóssil e geoquímicas indicam condições climáticas relativamente úmidas ao longo do período registrado. Apesar destas condições de umidade, a atuação de fogos foi frequente e é uma das razões apontadas para a dominância de savana ao invés de floresta na região de estudo. Considerando que as condições climáticas foram geralmente úmidas, infere-se que estes fogos provavelmente foram causados pelas atividades antrópicas. Mesmo atualmente, os fogos impedem a expansão da floresta sobre as áreas de savana. Além disso, os solos arenosos e hidromórficos também podem atuar como um controle edáfico para manter delineado o limite atual entre os ecossistemas de floresta e savana.

Palavras-chave: frequência do fogo, Holoceno tardio, Roraima-Brasil, dinâmica da vegetação.

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