Lateglacial and Holocene vegetation and climate change in lowland Colombia.

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Chapter 5

LATE QUATERNARY SAVANNA HISTORY OF THE COLOMBIAN LLANOS ORIENTALES FROM LAGUNAS CHENEVO AND MOZAMBIQUE: A TRANSECT SYNTHESIS

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ABSTRACT

A 7000-YR POLLEN RECORD OF A 90-CM CORE FROM CHENEVO (4°05′N, 70°21′W, 150 m alt.) AND A 3500-YR POLLEN RECORD OF A 285-CM CORE FROM Mozambique (3°58′N, 73°03′W, 175 m alt.) both from the savannas of the Llanos Orientales, Colombia, are presented. The records show dynamics between open savanna (Poaceae, Cyperaceae), woody savanna (Byrsonima, Curatella, Didymopanax), palm swamp (Mauritia, Mauritiella), forest and gallery forest taxa. These reflect plant available moisture, i.e. precipitation and length of the dry season, and more latterly human impact.

The record from Chenevo shows the following development: from 7260 to 6930 ¹⁴C yr BP open savanna vegetation and gallery forest along the drainage system, from 6930 to 4000 ¹⁴C yr BP forest and gallery forest expanded, from 5500 ¹⁴C yr BP Mauritia palm forest increased and particularly so from 4000 to 2380 ¹⁴C yr BP also in combination with gallery forest expansion, from 2380 ¹⁴C yr BP to present day gallery forest, Mauritia and Mauritiella palm forest is most abundant.
The record from Mozambique is hampered by $^{14}$C reversals, but appears to show the following development: from 3440 to 610 $^{14}$C yr BP abundant *Mauritia* swamp forest, from 600 $^{14}$C yr BP *Mauritia* swamp forest was replaced by gallery forest in which *Byttneria*, *Mimosa* and Sapindaceae are present, from 600 to 350 $^{14}$C yr BP gallery forest replaced woody grass savanna, during the last 350 $^{14}$C yr BP savanna increased and gallery forest decreased; as *Cecropia*, *Mauritia* and *Zea mays* point to human impact. Vegetation dynamics at the base of the core relate to changes in the local drainage system while more recent change relates to human impact.

Comparison of pollen records from six savanna lakes located along 400 km east west transect (Sardinas, Angel, El Piñal, Carimagua, Chenevo and Mozambique) shows the following regional vegetation and climate development. From 18,000 to 10,700 $^{14}$C yr BP patchy gallery forest, non-permanent lake conditions and maximum abundance of grasses reflect low precipitation and long dry seasons. From 10,700 to 9700 $^{14}$C yr BP gallery forest expansion reflect a more humid climate. From 9700 to 5800 $^{14}$C yr BP grasslands were maximally expanded reflecting dry climatic conditions. From 5800 to 3800 $^{14}$C yr BP gallery forest increased; this is thought to be indicative of higher precipitation and possibly a shorter dry season. Around 4000 $^{14}$C yr BP the savanna ecosystem changed in all records presented: particularly the palms *Euterpe/Geonoma Mauritia* and *Mauritiella*, became abundant in the savanna ecosystem, this may be indicative of human impact on the savanna ecosystem.

5.1 INTRODUCTION

The savannas east of the northern Andes are mainly shared between Colombia and Venezuela; the Llanos Orientales of Colombia, and the Orinoco savannas of Venezuela (Sarmiento and Monasterio, 1975; Botero, 1999) and constitutes the main tropical savanna in northern South America (Figure 5.1). The presence of savanna relates to climate (Sarmiento, 1968), soil conditions (Goosen, 1971), fire regime (Vareschi, 1960), and human activities (Puig, 1972). Wijmstra and Van der Hammen
Figure 5.1. Map showing the geographical location of sites Laguna Mozambique and Laguna Chenevo in the Llanos Orientales of Colombia, and other pollen sites mentioned in the text.
(1966) made the first palynological study in the Llanos Orientales of Colombia: the pollen record of Laguna de Agua Sucia (3°35'S, 73°31'W, 300 m altitude) showed a first insight of the vegetation and climatic history from approximately 5100 14C yr BP to the present. Recently, a number of savanna lakes located along an east-west transect through the Colombian Llanos Orientales were studied: Laguna Angel (4°28'N, 70°34'W, 200 m altitude) and Sardinias (4°58'N, 69°28'W, 80 m altitude), Carimagua (4°04'N, 70°14'W, 180 m altitude), El Piñal (4°04'N, 70°14'W, 180 m altitude) and Loma Linda (3°18'N, 73°23'W, 310 m altitude) by Behling and Hooghiemstra (1998, 1999, 2000); Laguna Carimagua-Bosque (4°04'N, 70°13'W, 180 m altitude) by Berrió et al. (2000); and Laguna Las Margaritas (3°23'N, 73°26'N, 290 m altitude) by Wille et al. (submitted). Most records cover the period from 12,000 to 2000 14C yr BP, only record El Piñal extends to the last glacial period. Oxidation of lake sediments during periods of low lake-levels is responsible for a lack of most recent sediment accumulation.

Other studies of neotropical savanna history include savanna in British Guyana (Van der Hammen, 1963), the Rupununi savannas (Wijmstra and Van der Hammen, 1966) and the Gran Sabana of Venezuela (Rull, 1992). A recent synthesis of savanna history by Behling and Hooghiemstra (2001) investigated Late Quaternary savanna dynamics north and south of the Amazonian rain forest.

We present here a new record from the Carimagua area, and a new pollen record from the yet unstudied western part of the Llanos Orientales. This is strongly influenced by numerous rivers that originate in the Eastern Cordillera combining from Río Meta, consequently river dynamics cause local environmental change superimposed on the regional climate evolution. The record of Laguna Mozambique appears to cover the last 3450 14C yr BP, the record of Laguna Chenevo shows the last 7260 14C yr BP. This paper will document the savanna history in a new area of the Llanos Orientales to evaluate the savanna history of the Carimagua area presented in earlier papers. Finally, regional climatic change will be placed in a wider context in which migration of the Intertropical Convergence Zone (ITCZ) plays an important role.
5.2 ENVIRONMENTAL SETTING, MODERN VEGETATION AND CLIMATE

The Llanos Orientales is located in the northeastern part of Colombia and extends from the Eastern Cordillera of the Andes as far east as the Orinoco River at the border with Venezuela (Figure 5.1). The area covers about 1,500,000 km² and includes different types of savanna; relict savanna forest, floodplain savanna, and seasonally flooded savanna (FAO, 1965; Castillo, 1992; Rangel et al., 1995) (Figure 5.2). According to Goosen (1971) the present surface of Llanos Orientales dates from the late Pleistocene with alluvial sediments transported from the Eastern Cordillera. The main landscape features in the study area are piedmont, alluvial fans, and elevated plains (Rangel et al., 1997).

Laguna Mozambique (3°58'N, 73°03'W, 175-m altitude; Figure 5.3) is located in Meta province close to Río Metica. The lake lies about 30 km south of the Río Metica and Río Humea confluence forming the Río Meta, which drains to the northeast into the Orinoco basin. The distance to Villavicencio, located at the foothills of the Eastern Cordillera, is about 80 km. The lake is 8 km² and generally shallows (50-cm water depth). The area regularly floods suggesting that the lake was originally part of the drainage system and became isolated from the main river during the middle Holocene.

Laguna Chenevo (4°05'N, 70°21'W, 150 m altitude, Figures 5.3a and 5.3b) is also located in Meta province but 175 km more to the east at some 15-km distant from the present course of the Río Meta (Figure 5.1). Laguna Chenevo lies in an area where patches of savanna forest and gallery forest are frequent and lies close to the earlier studied lakes of El Piñal (some 10-km distance) and Carimagua (some 15 km distant).

Laguna Chenevo (1.5 km²) seems to reflect part of an old meander. In the centre of the lake water depth is about 2.5 m.

FAO (1965), Blydenstein (1967), Cuatrecasas (1989), Castillo (1992) and Pinto-Escobar (1993) have studied the modern vegetation of the Llanos Orientales of Colombia. Various types of savanna vegetation, which relate
Figure 5.2: Schematic cross section through the Colombian savanna area showing the relationship between landscape topography, drainage system and vegetation.
Figure 5.3 (b) View on Laguna Chenevo showing palms of *Mauritia flexuosa* (Photo: H. Hooghiemstra)
to geomorphological setting, have been identified (FAO, 1965; PRORADAM, 1979). On the seasonally inundated alluvial fans a herb community dominated by *Trachypogon vestitus* (Poaceae) and *Axonopus purpusii* (Poaceae) is found. On the well-drained higher plains, a grassy vegetation dominated by *Paspalum pectinatum* and *Trachypogon vestitus* is found (Goosen, 1971; Rangel et al., 1995). According to Cuatrecasas (1989), the most important genera of the grass savanna are *Andropogon, Aristida, Axonopus, Eragrostis, Paspalum* and *Ctenium*. Characteristic shrubs are *Clitoria, Miconia, Pavonia, Sida, Tibouchina* and *Waltheria*. Characteristic low trees of higher stature are *Byrsonima crassifolia, Curatella americana*, and *Palicourea rigida*. Dense gallery forest occurs along the river borders, this also extend to areas that may have served as drainage channels in the past, locally called 'esteros' (Goosen, 1971). In areas with stagnant water floating vegetation occurs characterised by *Eichornia azurea* and *Pistia stratiotes*. Other aquatics and taxa of wet soils are *Eriocaulon* sp., *Limnocharis flava*, *Neptunia natans, Polygala* sp., *Rynchospora* sp., *Syngonanthus* sp., *Typha angustifolia*, and *Utricularia* sp.

Annual precipitation in the Llanos Orientales varies from 1200 to 2800 mm (Blydestein, 1967; Snow, 1976). The rainy season is from April to November, with most precipitation falling in July (370 mm) when the meteorological equator (ITCZ) has its northernmost position. The dry season, locally called 'sequia', occurs from November to February; January is the driest month with 25 mm precipitation (Lowy and Rangel, 1993). The mean annual temperature is 26-27°C, with less than 3°C variation between monthly means. The small annual temperature amplitude contrasts with the daily variation of 10° to 15°C (maximum mean temperature of 33.6°C and a minimum mean temperature of 19°C; Rangel et al., 1995).

Archaeological evidence for the earliest human impact on the Colombian and Venezuelan savannas comes from the Orinoco River area and was dated 9000 ¹⁴C yr BP (Barse, 1989, 1995), and from the area of San José del Guaviare 7000 ¹⁴C yr BP (Correal et al., 1990). In the Colombian savannas several archeological sites have been studied by Marwitt (1973), Reichel-Dolmatoff (1974), Giraldo (1976), Mora and Cavelier (1983, 1985), and Alarcon and Segura (1997); in general these studies indicate that Pre-Co-
lombians were living close to the rivers cultivating crops (*Zea mays*) and other plants from the gallery forest like *Anadenanthera peregrina* (Caesalpinaceae), *Attalea insignis*, and *Bactris gasipaes* (Arecaceae) since the middle Holocene.

## 5.3 METHODS

The sediments of both lakes were cored from a floating raft in the centre of the lake using a modified Livingstone piston corer. The recovered sediment settings are 5 cm in diameter and 100 cm long, these were retained in the aluminium tubes used during coring. Within three weeks after collection, the cores were stored in a cold and dark room (4°C) at the Hugo de Vries Laboratory.

Seven bulk samples of 1 cm³ from Laguna Mozambique and six samples from Laguna Chenevo were radiocarbon dated by accelerator mass spectrometry (AMS) at the Van der Graaf Laboratory of the University of Utrecht (Van der Borg et al., 1987) (Table 5.1). To quantify the organic carbon content we measured loss on ignition (Bengtsson and Enell, 1986). For pollen analysis, samples (0.5 cm³) were taken at 5 cm intervals along the core from Mozambique, and at 2.5 cm intervals along the core from Chenevo. Pollen was concentrated using the standard treatment of sodium pyrophosphate, acetalolysis, and heavy liquid separation by bromoform (Faegri and Iversen, 1989). Before chemical treatment, exotic *Lycopodium* spores were added to each sample for calculation of the pollen concentration and pollen influx values. Most of the samples were counted up to a minimum of 300 pollen grains, excluding grains of aquatic taxa, fern spores, fungal spores and algae. Carbonised particles in the pollen slides were not quantified because during the heavy liquid separation a significant, but unknown, number of the charcoal particles are eliminated.

For identification of pollen and spores, morphological descriptions published by Behling (1993), Herrera and Urrego (1996), Hooghiemstra (1984), Roubik and Moreno (1991) and the reference collections of the Hugo de Vries Laboratory were used. According to Behling and Hooghiemstra (1998;
Table 5.1. List of AMS radiocarbon dates on the samples from Mozambique and Chenevo, Llanos Orientales, Colombia

1999; 2000) pollen taxa were classified into the following ecological groups: (1) trees of forest and gallery forest, (2) shrubs and trees of savannas, (3) savanna herbs, (4) aquatics and (5) ferns. As some taxa have different ecologies in the different lake settings the broad ecological groups to which we assign our pollen taxa is noted in Table 5.2. For example Cyperaceae as assigned as a savanna herb at Chenevo and as aquatic at Mozambique where it is found around the lake margin. We also established an ecological group including arboreal taxa with a main distribution in the Eastern Cordillera; in tropical lowland studies these taxa are often referred to as 'Andean taxa' (Gentry, 1993). However, such taxa probably do not indicate the presence of taxa from montane ecosystem: grains of \textit{Podocarpus} and \textit{Weinmannia} may be easily wind-transported from large distances, grains of \textit{Alnus} are often transported over large distances from montane areas by rivers (Van der Hammen and Hooghiemstra, 2000), while \textit{Hedyosmum} is not restricted to Andean vegetation belts but is also a common component of savanna forest (Rangel et
Trees of Forest & Gallery Forest

Acalypha (M, Ch)
Aegiphila-type (Ch)
Ailchornea (M, Ch)
Alibertia-type (M, Ch)
Anacardiaceae (M, Ch)
Annona (Ch)
Annonaceae (Ch)
Amanoa (Ch)
Apocynaceae (M, Ch)
Bauhinia (M)
Bignoniaceae (M)
Byttneria (M, Ch)
Caesalpinaceae (Ch)
Casearia-type (M, Ch)
Cassia-type (M)
Cecropia (M, Ch)
Celtis-type (M, Ch)
Clusia (M, Ch)
Coccoloba-type (M)
Connarus-type (M)
Convolvulaceae (Ch)
Croton (M, Ch)
Euterpe/Geonoma-type (M, Ch)
Desmodium-type (M)
Dioclea-type (M)
Euphorbiaceae (M)
Fabaceae-I (M, Ch)
Fabaceae-II (M, Ch)
Fabaceae-III (Ch)
Genipa-type (M)
Gustavia-type (M)
Hyeronima (M, Ch)
Ilex (M, Ch)
Lecythidaceae (M)
Loranthaceae (M)
Mabea (M)
Macrobolium (M, Ch)
Malpighiaceae (M, Ch)
Malvaceae (M, Ch)
Marila-type (Ch)
Mauritia (M, Ch)
Mauritiella (Ch)
Mecardonia-type (M)
Melastoma./Combretaceae (M, Ch)
Menispermacae (Ch)
Mimosa (M)
Mimosaceae (Ch)
Myrsine (M, Ch)
Myrtaceae (M, Ch)
Oreopanax (M)
Pavonia-type (M)
Peperomia (Ch)
Pera-type (Ch)
Piper (M)
Pilea (M)
Protium (M, Ch)
Psychotria-type (M, Ch)
Rubiaceae (M, Ch)
Sabicea-type (Ch)
Sapindaceae (M, Ch)
Sapium (M)
Sapotaceae (M, Ch)
Sloanea-type (M, Ch)
Socratea-type (Ch)
Solanaceae (Ch)
Solanum (Ch)
Spermacoce (M)
Spondias (M)
Sterculiaceae (Ch)
Symphonia (Ch)
Symplocos (M, Ch)
Tapirira (Ch)
Tournefortia (M)
Trema-type (M, Ch)
Virola (M, Ch)
Vismia (M, Ch)
Xylosma-type (M)
Zanthoxylum (M)
Savanna Shrubs & Trees
Byrsonima (M, Ch)
Curatella (M)
Didymopanax (M, Ch)

Savanna Herbs
Althernantera (M)
Amaranthaceae/Chenopodiaceae (M)
Asteraceae subf. Asteroideae (M, Ch)
Asteraceae subf. Liguliflorae (M)
Borreria (M, Ch)
Cyperaceae (Ch)
Ipomoea (Ch)
Lamiaceae (M, Ch)
Plantago (Ch)
Poaceae (M, Ch)
Spermacoce (Ch)
Umbelliferae (Ch)
Zea mays (M, Ch)

Andean Taxa
Alnus (M, Ch)
Hedyosmum (M)
Myrica (M)
Podocarpus (M, Ch)
Weinmannia (M, Ch)

Aquatics
Cabomba (Ch)
Cuphea (Ch)
Cyperaceae (M)
Isoëtes (M, Ch)
Ludwigia (M, Ch)
Plantago (M)
Polygonum (M, Ch)
Potamogeton (M)

Unknowns
c3p3-Oblate (Ch)
c3p3-Reticulate (M, Ch)

Fern Spores
Asplenium (Ch)
Cyathea (M, Ch)
Pytiogramma (M, Ch)
Selaginella (M, Ch)
Monolet e psilate < 50 μm (M, Ch)
Monolet e verrucate <50 μm (M, Ch)
Trilete psilate (M, Ch)

Fungal Spores
Gelasinospora (M, Ch)
Tetraploa aristata (M)

Algae
Botryococcus (M, Ch)
Pediastrum (M, Ch)
Gomphrena (M)
Pseudoschyzoea circula (Ch)
Spirogyra (Ch)
Zygnemataceae (Ch)

Sagittaria (M, Ch)
Utricularia (M, Ch)
Xyris (M)

Table 5.2. List of identified fossil pollen and spore taxa in Mozambique (M) and Chenevo (Ch), arranged after ecological preference.
Also, a comparative study of four savanna lakes isolated in different degrees from the surrounding grass savannas indicate the higher the degree of isolation by gallery forest, the less savanna pollen is represented in the lake sediments pollen assemblages (Berrío et al., 2000). For calculation of pollen sums, cluster analysis, and data plotting, TILIA, CONISS, and TILIAGRAPH software were used, respectively (Grimm, 1987). Pollen zones were placed at depths where significant changes in frequency of important taxa and/or changes in the composition of the pollen assemblages occurred. Records of the most frequent individual pollen and spore taxa are presented in pollen percentage diagrams (Figures 5.4 and 5.6), whereas the records of broad ecological groups, pollen concentration, pollen influx, pollen sums and the cluster analysis dendrogram are shown in a ‘diagram of sums’ (Figures 5.5 and 5.7).

5.4 RESULTS

5.4.1 Stratigraphy

The downcore changes in lithology of both sediment cores, shown is the pollen diagrams (Figures 5.5 and 5.7) is as follows:

**Mozambique**

20-30 cm: very soft dark grey clay  
30-200 cm: compact dark grey clay with abundant rootlets and plant remains at 145-130 cm and 200-176 cm, woody fragments 135 cm  
200-225 cm: dark brown peaty clay with carbonised particles, woody fragments at 200 cm  
225-260 cm: transition to light grey clay, some sand  
260-275 cm: dark sand

**Chenevo**

0-45 cm: peaty, dark grey clay with abundant rootlets and some sandy horizons at 25 cm  
45-60 cm: dark sandy grey clay without rootlets  
60-90 cm: compact dark grey clay with very few rootlets
Figure 5.4. Percentage pollen diagram from Chenevo, Llanos Orientales, Colombia
Figure 5.5. Summary pollen diagram from Chenevo including pollen concentration and pollen influx records, and the cluster analysis dendrogram.
Figure 5.6. Percentage pollen diagram from Mozambique, Llanos Orientales, Colombia.
Figure 5.7. Summary pollen diagram from Mozambique including pollen concentration and pollen influx records, and cluster analysis dendrogram.
5.4.2 Chronological control

The ages of the bulk radiocarbon samples of the Mozambique core do not increase with depth and need some discussion. The oldest ages of $4805 \pm 47 \text{^{14}C yr BP}$ and $5040 \pm 50 \text{^{14}C yr BP}$ are from sediments in the upper 70-cm of the core. As three samples of the core interval 125 to 203 cm have an age of less than 1000 years, we conclude that sediments at 70 cm and 20 cm core depth may have been contaminated with re-worked water-transported organic material. The lithological sequence also indicates that flood deposits are included: the upper 30 cm of sediment has not yet consolidated and may represent a period of rapid sediment accumulation, including allochthonous material. This also explains the low pollen content of the upper three samples (Figure 5.7). The sediments between 30 and 106 cm do not contain plant fragments and rootlets; this may also be indicative of mainly allochthonous sediments. The relatively high contribution of 'Andean pollen taxa', in particular *Alnus*, common in the river accompanying forest, and the pioneer tree *Cecropia*, common on young soils after rivers have retreated, supports the view that sediments in the upper 100 cm include a significant part of river-transported sediments. The maximum savanna signals around 200-cm and maximum forests signal around 135-cm (Figure 5.7), coincide with a significant amount of wood debris and horizontally deposited leaves. We interpret these as periods during which river supplied sediments that accumulated rapidly; around 200-cm the main source area was the savanna, whereas around 135 cm the river apparently supplied material derived from a forested area. The radiocarbon ages between 125 and 272-cm show increasing age with depth, we use these to calculate the age of the identified pollen zones. The age of the bulk radiocarbon samples of Chenevo increases with depth and leaves no doubt about the robustness of the calculated age-depth relationship.

5.4.3 Description of pollen diagram Laguna Mozambique

In pollen zone MZQ-I (275-203 cm, 15 samples) the record shows high percentages of pollen from savanna herbs (45-55% in the lowermost part and 45-65% in the uppermost part), mainly represented by Poaceae (52%),
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Cyperaceae (3-27%) and Asteraceae subf. Asteroideae (6% in the lowermost part). Shrubs and trees from the forest and gallery forest (43-60%) are primarily represented by *Mauritia*-type (38%), *Acalypha* (10%), *Alchornea* (5%), Sapindaceae (5% in the uppermost part), *Mabea*-type, Melastomataceae, and Moraceae/Urticaceae (less than 5%). Pollen grains of savanna shrubs and trees are represented with 0.5-4% only and include pollen grains of *Byrsonima* and *Didymopanax*. Taxa with Andean affinity are well represented in the middle part of zone MZQ-I, mainly by *Hedyosmum* (3%). Mainly Cyperaceae (30%), *Ludwigia* (7%), *Polygonum* (5%) and *Sagittaria* 5% represent aquatic taxa. Total carbon values increase from 2% at the beginning of the zone to 39% at the end.

Pollen zone MZQ-II (203–153 cm, 10 samples) is characterised in the lower part by highest percentages of savanna herbs (83%), mainly by Poaceae (75%). The contribution of shrubs and trees from forest and gallery forest increases from 15% to 60% at the upper part of this zone. Main taxa are *Alchornea* (5-30%), Sapindaceae (0.3-32%), *Byttneria*-type (5%), Moraceae/Urticaceae (5%), and Myrtaceae (8%). Pollen taxa with values less than 5% are *Mauritia*-type, *Acalypha*, *Mabea*-type, Melastomataceae, *Mimosa* and Fabales. Pollen of savanna shrubs and trees (2-7%) are more common than the previous zone: main taxa are *Byrsonima* (6%), *Curatella*-type (1%) and *Didymopanax*-type (1%). Pollen grains from Andean forest taxa are hardly represented (1%). We registered 1% of *Zea mays*. Aquatic taxa are very common (10-50%), and include *Polygonum* (10%) and *Ludwigia* (1%). Total carbon values reach highest values of 49%.

Pollen zone MZQ-III (153-20 cm, 25 samples) is not described. No further zonation was made due to the presence of fluvial sediments that may have provided a 'regional overprint' on top of the 'local pollen assemblages' due to uncertainties of its provenance. Total carbon values are mostly less than 5%.

5.4.4 Description of pollen diagram Laguna Chenevo

Pollen zone CHV-Ia (90-67.5 cm, 9 samples) is characterised by high values of savanna herbs (60%) mainly represented by Poaceae (45%) and
Cyperaceae (10%). Gallery forest shows highest values just at the beginning of the zone (55%), with Moraceae/Urticaceae-type and Alchornea (6%), Acalypha (8%), Myrtaceae and Melastomataceae/Combretaceae (4%) as most important taxa. Savanna shrubs and trees show percentages less than 4%. Aquatics (14%) are well represented by Sagittaria (6%), Cuphea (5%) and Ludwigia (3%). Total carbon values are ca.5%.

In pollen zone CHV-Ib (67.5-52.5 cm, 7 samples) savanna taxa decrease gradually to 25%; Poaceae (40-20%) and Cyperaceae (6%) are the main taxa. Trees and shrubs of the gallery forest increase from 49% to 70%: Mauritia (35%) at the end of the zone, Moraceae/Urticaceae-type (6%), Cecropia increases values from 2% to 5%, but Acalypha and Alchornea decrease to 2% and 6%, respectively. Other important taxa such as Croton, Fabaceae-I and Macrolobium-type remain at the same values as the previous pollen zone. Aquatics fluctuate to 18% as a maximum, Sagittaria (15%) being the main element. The total carbon content decreases from 5% to 3%.

Pollen zone CHV-II (52.5-30 cm, 9 samples) is characterised by shrubs and trees gallery forest (79-70%). Mauritia is increasingly dominant (46%). Cecropia reach maximum values of 7%, Acalypha decreases from 15% to 5% at the end of the zone. Virola is recorded for the first time in the record at low values (2%), also Myrtaceae is present with 2%. Moraceae/Urticaceae-type shows constantly low values of 2%. Alchornea (5%) and Melastomataceae/Combretaceae (6%) show lower values in the middle of the zone (6-1%). The savanna shrubs and trees (Didymopanax and Byrsonima) are present at low values (1-2%). Savanna herbs show 15-25%, mainly Poaceae, show decreasing values from 20% to 10%. Cyperaceae continues to record about 2%. Among aquatics taxa Sagittaria keeps values of 5%, Cuphea varies between 2% and 1%, and Ludwigia shows 4%. Total carbon shows similar values as in the previous zone (6%).

In pollen zone CHV-III (30-0 cm, 12 samples) shrubs and trees of forest and gallery forest show maximum percentages of 85%. Mauritia records about 45%, Mauritiella 8% for first time in the record. Also Moraceae/Urticaceae-type (9%), Cecropia (6%), Acalypha (14%) and Virola (9%) show high values in this zone. Myrtaceae drops to 1%, the lowest value of the record. Melastomataceae/Combretaceae and Alchornea are present with 4%.
Savanna shrubs and trees, mainly *Didymopanax* (2%) and *Byrsonima* (1%) are rare. Savanna herbs (19%), consisting of mainly Poaceae (9%) and Cyperaceae (4%), reach the lowest values of the pollen record. Aquatics (10-2%) also show the lowest values of the record. Nevertheless *Sagittaria*, *Cuphea* and *Ludwigia* are still present at 4%, 2% and 1%, respectively. Total carbon reaches maximum values of 20%.

5.5 ENVIRONMENTAL RECONSTRUCTION AND DISCUSSION

We present here the environmental reconstruction of the eastern savanna area from Chenevo, and the western part of the savanna area from Mozambique. In the following section we compare both records with the earlier published records of Carimagua, Carimagua-Bosque, El Piñal, Angel and Sardinas to arrive at an environmental reconstruction along a 400 km long transect through the Llanos Orientales.

5.5.1 Laguna Chenevo, eastern Llanos Orientales

During the period of from 7260 to 6930 $^{14}$C yr BP (zone CHV-Ia) opens savanna vegetation, dominated by grasses, Cyperaceae and *Byrsonima* was common. The transition from sand to dark grey clay (at 90 cm) reflects the period when the lake became isolated from the regional drainage system. Presence of forest and gallery forest taxa (40-50%), including *Alchornea*, *Acalypha*, *Croton*, Moraceae/Urticaceae, Myrtaceae and Melastomataceae/Combretaceae indicate that forested areas were common along the drainage system. From the beginning of the record aquatics, including *Cuphea*, *Ludwigia* and *Sagittaria* were common in this shallow lake in which also the algae *Botryococcus* and Zygnemataceae occurred. Low pollen influx values support the relatively high sedimentation rate during this period. The LOI record shows values of 5% indicating that total carbon content of the lake sediments is low.

During the period from 6930 to 4000 $^{14}$C yr BP (zone CHV-Ib) forest and gallery forest expanded continuously in the surroundings of Chenevo. Around 5500 $^{14}$C yr BP sediments became more sandy, aquatics rarer, and
Mauritia palm forest increased rapidly, all reflecting more dynamic conditions and possibly human disturbance. Around 5500\(^{14}\)C yr BP there is also a change in the composition of forest: Croton and Alchornea decreased markedly whereas Acalypha and Cecropia became more frequent, this change may also point to more dynamic conditions. The replacement of savanna by forest and gallery forest may be overestimated; Berrió et al., (2000) showed that the pollen signal of savanna is under-represented in lake sediments when the lake is totally surrounded by a zone of gallery forest and ‘isolated’ from the savanna ecosystem, even when proximal to the core site. The pollen influx values increased markedly. The LOI values record the lowest values (3\%) in this core which corresponds with high sand content.

During the period of from 4000 to 2380\(^{14}\)C yr BP (zone CHV-II) Mauritia palm swamp and gallery forest (including Acalypha, Alchornea, Cecropia, Macrolobium, Melastomataceae-Combretaceae, Moraceae-Urticaceae, Myrtaceae, and Protium) were abundant around Chenevo. From this time onward Cecropia is an important component of the canopy. Aquatic taxa continue at the same level suggesting the water-level does not change significantly. Two radiocarbon dates around 2400 \(^{14}\)C yr BP show that sediment accumulation is high from 40 to 30 cm; this is supported by the low pollen concentration values in this core interval. LOI values increase slightly to 5\% indicating a low carbon accumulation in the lake system.

From 2380 \(^{14}\)C yr BP to today (zone CHV-III) forest and gallery forest is most abundant. The trees Virola and Trema and the palms Mauritiella and Euterpe-Geonoma become frequent for the first time in the record, whereas Myrtaceae almost disappear. Other main arboreal taxa are Acalypha, Cecropia, Mauritia, Melastomataceae-Combretaceae and Moraceae-Urticaceae. In the open savanna Didymopanax is now more frequent than Byrsonima. The high abundance of palms, in particular Mauritia, which is nowadays of significant economic importance for local people, possibly points to early human impact. Presence of charcoal particles in this part of the core points to an intensified fire regime, possibly of anthropogenic origin. However, impoverishment of the drainage system in this area may have led to extensive Mauritia and Mauritiella swamp forest (‘morichal’) which may ex-
plain the increased carbon content of the sediments (LOI values increase up to 18%). Higher water-level in Chenevo, is indicated by the decrease of aquatic vegetation.

5.5.2 Mozambique, western Llanos Orientales (Figures 5.6 and 5.7)

During the period from 3440 to 61014C yr BP (zone MZQ-I) Mauritia swamp forest was abundant around the lake. The lower 15-cm of sediments consists of dark sand possibly reflecting a period when the lake became isolated from the regional drainage system and was surrounded by a poorly drained swampy area in which Mauritia palm forest could expand. Abundant aquatics, mainly Ludwigia and Polygonum, indicate that this large lake was shallow water. Forest and gallery forest taxa (40-50%), mainly Aca-lypha, Alchornea and Melastomataceae/Combretaceae, indicate that gallery forest was common around the lake. Grass savanna, poor in woody taxa, may have reached the lake margin at some places. The tree Hedysmum was almost continuously present in the forest and gallery forest around the lake, as it is today (Rangel et al., 1995). Hedysmum in Amazonian lowland records of the last glacial has sometimes been classified to the category ‘Andean trees’ (i.e. cold-adapted taxa) and used to infer lower temperature conditions. Although this line of reasoning is still controversial (Van der Hammen and Hooghiemstra, 2000; Colinvaux et al., 2000), it is not valid at all in the savannas of the Llanos Orientales where Hedysmum is a natural component of the vegetation.

Around 60014C yr BP Mauritia swamp forest on poorly drained soil was almost totally replaced by gallery forest in which Byttneria, Mimosa, and Sapindaceae are new elements. Aquatic vegetation decreased and fungal spores, indicative of decomposition of exposed organic material, became abundant. A marked lowering of the water table is plausible, possibly in relation to improved drainage of the area, although drier regional climatic conditions cannot be excluded. The proximal location of the lake to the Rio Metica makes a change in the drainage capacity plausible. The abundant wood fragments and leaves between 200 and 176 cm is further indicative of a sudden riverine supply of sediments olden
with plant debris; we suggest the lake became temporarily in contact with the regional drainage system. Expanding gallery forest from 600 to 350 \(^{14}\)C yr BP (zone MZQ-II) replaced woody grass savanna, mainly consisting of Poaceae and woody *Byrsonima*. Sediments are rich in total organic carbon (LOI values of 30-48%).

During the last 350 \(^{14}\)C yr BP (zone MZQ-III) some 1.5 m of sediment accumulated, consequently the pollen concentration and total organic carbon content are low. In the category 'Andean trees' *Alnus* and *Weinmannia* are now present; pollen of these true Andean taxa (Van der Hammen and Hooghiemstra, 2000) indicate supply of riverine water originating from the Eastern Cordillera to the lake, possibly during episodes of massive inundations of the area between Lake Mozambique and the Río Metica. Such inundation phases also explain the increased sediment supply to the lake, the wood fragments and leaves in the 145-130 cm interval and the radiocarbon reversals, possibly based on allochthonous organic material (see the discussion of time control). In the uppermost 125 cm of the core, representing the last 300 \(^{14}\)C yr, savanna increased with a concomitant gallery forest decrease. The contribution of *Alchornea* decreased whereas *Cecropia* became more abundant: we interpret this change as evidence of increased human impact. Furthermore, the presence of *Zea mays* and *Mauritia* palms during the last few hundreds of years indicates areas of active cultivation close to the lake.

5.6 SYNTHESIS OF LATE PLEISTOCENE SAVANNA DYNAMICS OF THE LLANOS ORIENTALES

In this section we discuss pollen records of Sardinas, Angel, El Piñal, Carimagua, Chenevo and Mozambique (Figure 5.8a and 5.8b) to provide a regional synthesis of ecosystem dynamics.

Savanna lakes most distant from the Eastern Cordillera (Sardinas, Angel, El Piñal, Chenevo, Carimagua) are characterised by slow sediment accumulation (70-90 cm of sediments), whereas lakes located in floodplain close to the Eastern Cordillera (Mozambique) accumulate great sediment
Figure 5.8 (a) Main percentage pollen diagrams of 6 savanna (here the first 3) lakes in the Llanos Orientales located along an east-west transect. Radiocarbon time control of each core and inter-core correlation is shown.
Figure 5.8 (b) Main percentage pollen diagrams of 6 savanna (here the last 3) lakes in the Llanos Orientales located along an east-west transect. Radiocarbon time control of each core and inter-core correlation is shown.
depths (2-3 m). Lakes located near the Eastern Cordillera (Loma Linda and Las Margaritas), where thick accumulations of clays and sands are dissected by more recent drainage systems, are characterised by sediments up to 9 m depth (Behling and Hooghiemstra, 2000; Wille et al., submitted). The record at El Piñal expands to the Last Glacial Maximum (LGM), while Sardinas includes part of the Lateglacial; Holocene records from Angel, Carimaguá and Chenevo expand to 10,000, 8000, and 7000 $^{14}$C yr BP, respectively. The Mozambique record is the shortest with sediments of some 3500 $^{14}$C yr BP.

Depending on plant-available moisture we observe changes between open grass savanna, woody savanna, palm swamp and gallery forest. From 18,000 to 10,700 $^{14}$C yr BP at El Piñal scarce gallery forest, non permanent lake conditions, and maximum abundance of grasses reflect low precipitation and long dry seasons. From 10,700 to 9700 $^{14}$C yr BP at El Piñal and Sardinas gallery forest expanded slightly. This may indicate that climate became more humid as is also recorded at Lake Valencia (Venezuela) between 11,000 and 9000 $^{14}$C yr BP (Bradbury et al., 1981; Leyden, 1985); Martin et al., (1997) explained this resulting from a precession-forced northward shift of the ITCZ. From 9700 to 5800 $^{14}$C yr BP (El Piñal, Sardinas, Angel, Carimaguá, and Chenevo) savanna expanded indicating dry climatic conditions. Lake Valencia documents also dry climatic conditions from 8000 to 5800 $^{14}$C yr BP (Bradbury et al., 1981). From 5800 to 3800 $^{14}$C yr BP (Sardinas, Angel, Carimaguá, and Chenevo) the area of gallery forest increased, this may be indicative of higher precipitation and possibly also shorter dry seasons. However, El Piñal does not register this change, indeed the site is relatively unresponsive being located within an area where edaphic conditions buffer climatic changes. Around 4000 to 3500 $^{14}$C yr BP the savanna ecosystem substantially changed in all records: the palms *Mauritia, Mauritiella, Euterpe/Geonoma* became abundant in the savanna ecosystem. This change was dated around 4000 $^{14}$C yr BP at Sardinas (Behling and Hooghiemstra, 1998), around 4500 $^{14}$C yr BP at Angel (Behling and Hooghiemstra, 1998), around 4000 $^{14}$C yr BP at Carimaguá (Behling and Hooghiemstra, 1999), before 1800 $^{14}$C yr BP at Carimaguá-Bosque (Berrío et al., 2000), around 5500 $^{14}$C yr BP at Chenevo, before 3500 $^{14}$C yr BP at Mozambique, and around 2500 $^{14}$C yr BP at Loma Linda (Behling and
Hooghiemstra, 2000). This marked change in environmental conditions was also noticed in the pollen-based biome reconstructions for Colombia a change to wetter conditions was inferred between 4000 and 3000 $^{14}$C yr BP (Marchant et al., 2001). Dense stands of Mauritia occur along waterways, lake margins and on poorly drained swampy areas. The shorter palm Mauritiella grows in shallow water and surrounds several lakes in the Llanos Orientales. Although Mauritia is an indicator of higher moisture availability (Kahn, 1987; Kahn and de Granville, 1992; Henderson, 1995), Mauritia palms are also of great economic value for the local population. Therefore, we consider the prominent presence of Mauritia palm forest since 4000 $^{14}$C yr BP as indicative of more human impact on the savanna ecosystem, during a period of relatively moist (shorter dry season and/or increased precipitation).

Comparison of the main pollen diagrams shows a significant variation in the ratio between ‘pollen from savanna vegetation’ and ‘pollen from gallery forest’. As discussed in Berrío et al., (2000) this relates to the degree to which savanna vegetation makes contact with the water body in the lake: apparently a forested fringe of some 0.5-1 km wide around a lake prevents pollen from savanna herbs being included in the lake sediments and, as a consequence, savanna extension is under-estimated. The lakes in the eastern Llanos Orientales are sensitive to changes in available moisture, i.e. changes in absolute precipitation and/or length of the dry season, and record transitions between open savanna and gallery forest. Laguna Mozambique and Laguna de Agua Sucia (Wijmstra and Van der Hammen,, 1966) are examples of lakes that lie within a wide floodplain. Such lakes suffer from periodically large-scale inundations that cause alternations between regional and local signals of environmental change. Fluvial supply of allochtonous pollen from the Cordilleras, coarse plant debris and wood fragments, and organic material may disturb the age-depth relationship of the sediments. Isolated depressions in the savanna of the southern Llanos Orientales, at close distance to the Eastern Cordillera are most sensitive to climatic change: high sediment accumulation rates allow for a high temporal resolution of the analyses, and dynamics between open savanna and closed gallery forest provides a sensitive recorder of environmental change.
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5.9 REFERENCES


