Lateglacial and Holocene vegetation and climate change in lowland Colombia.

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Chapter 4

LATE HOLOCENE HISTORY OF SAVANNA GALLERY FOREST FROM CARIMAGUA AREA, COLOMBIA

Juan Carlos Berrío, Henry Hooghiemstra, Hermann Behling and K. van der Borg

ABSTRACT

THE POLLEN RECORD OF A 65-CM LONG CORE LAGUNA CARIMAGUA-BOSQUE (4°04'N, 70°13'W) SHOWS THE LATE HOLOCENE ENVIRONMENTAL HISTORY FROM a lake located within the gallery forest of the savannas of the Llanos Orientales of Colombia. Nine AMS radiocarbon dates of the organic deposits show the core represents the period from c. 1300 ^{14}C yr BP to the present. The lake evolved from an active drainage system.

During the period from c. 1300 to 875 ^{14}C yr BP (zone CMB-Ia) *Mauritia*-dominated swamp and gallery forest was present dominated by *Cecropia*, and later also *Acalypha* and *Alchornea*. From 875 to 700 ^{14}C yr BP (zone CMB-Ib) the lake was completely surrounded by gallery forest. *Mauritiella* and *Cecropia* occurred around the lake. *Cecropia* pioneer forest reached its greatest abundance and became gradually replaced by a more species rich gallery forest, including *Acalypha, Alchornea, Euterpe/Geonoma,* Moraceae/ Urticaceae, Piperaceae, and *Virola*. From 700 to 125 ^{14}C yr BP (zone CMB-II) *Cecropia* lost its dominant role and *Mauritiella* palms became more frequent. Main vegetation categories were swamp forest, gallery forest, understory elements, savanna shrubs and trees, and grass savanna. From 125 ^{14}C yr BP to recent (zone CMB-III) plant diversity in the gallery forest became highest, *Mauritiella* became very abundant and among the savanna elements woody *Didymopanax* increased.

Comparison of 4 pollen records from savanna sites shows that pollen of savanna vegetation is markedly underrepresented in lake sediments when the lake lies within the gallery forest. As most of the drainage system of a savanna is hidden by gallery forest we expect also significant under-representation of the savanna ecosystem in river-transported pollen assemblages.

4.1 INTRODUCTION

For a long time the history of the savannas north of the Amazon basin was poorly known. Wijmstra and Van der Hammen (1966) published the first pollen records of this ecosystem from Laguna de Agua Sucia in the Colombian Llanos Orientales, and from the Rupuni savannas in Guyana (Wijmstra, 1971). A synthesis of the history of the neotropical savannas was published by Van der Hammen (1983). More recently Rull (1992, 1999) studied savannas in the Gran Sabana of Venezuela. During explorations in 1996 and 1997 by H. Hooghiemstra and H. Behling in the Colombian provinces of Meta and Vichada sediment cores were collected from over ten new locations in the savannas of the Llanos Orientales. Results from these cores have been published recently: Lagunas Angel and Sardinas (Behling and Hooghiemstra, 1998), Lagunas El Piñal and Carimagua (Behling and Hooghiemstra, 1999). Other pollen records concern Laguna Loma Linda (Behling and Hooghiemstra, 2000), Laguna Las Margaritas (Wille *et al.*, submitted), and Lagunas Mozambique and Chenevo (Berrío *et al.*, 2002.). Behling and Hooghiemstra (2001) published an overview and comparison of the savanna ecosystems north and south of the Amazonian rain forest.

The present paper aims to show the environmental history of the savanna ecosystem based on pollen record of Laguna Carimagua-Bosque and to compare the vegetation development with other pollen records from the Colombian Llanos Orientales. In particular we aim to compare records from two lakes at very close distance within a significantly different setting. Laguna Carimagua-Bosque (this paper) today is located in the gallery forest, whereas Laguna Carimagua (Behling and Hooghiemstra,

1999) at 3 km distance is surrounded by open savanna vegetation and only a few patches of *Mauritia*-dominated palm forest reach the lake shore. Finally we infer conclusions of more general value for the reconstruction of savanna environments from pollen records.

According to Sarmiento and Monasterio (1975) savannas are stable ecosystems, floristically dominated by grasses but also including herbs, shrubs, and some characteristic trees (such as *Curatella* and *Byrsonima*). Laguna El Piñal shows the longest record and reaches as far back in time as the last glacial maximum (LGM). It shows shifts in the contribution of open grass savanna, wooded savanna, and gallery forest, but the floral composition of these types seem to be relatively stable (Behling and Hooghiemstra, 1999). On the other hand, Beard (1953), Blydestein (1967), and Hills and Randall (1968) have supported the idea that the extension of savanna and savanna-forest is edaphically determined as a consequence of poor drainage in combination with strong seasonal precipitation. Moreover, gallery forest can occur in the lower parts of the drainage system if water is available to wet the soil during the dry season (Monasterio and Sarmiento, 1971).

4.2 STUDY AREA

Laguna Carimagua-Bosque (4° 04'N, 70° 13'W, Province of Meta; 180 m altitude) lies in the Llanos Orientales and is part of a series of studied sites along a 500 km long west to east transect (Fig. 4.1). The distance to the lagunas Carimagua and El Piñal is c. 3 km, and 22 km respectively (Behling and Hooghiemstra (1998). Other lakes that were studied palynologically are lagunas Sardinas and Angel (Behling and Hooghiemstra, 1998); both more than 100 km distant from the site Carimagua-Bosque. The distance to the foot of the Eastern Cordillera at Villavicencio is c. 270 km. Laguna Carimagua-Bosque is a shallow lake, maximally 1-2 m deep with a diameter of c. 150 m (Fig. 4.2). It is located in an extended slightly undulating savanna landscape. Maximum difference in elevation is c. 50-80 m, but in the surroundings of the site Carimagua-Bosque it is 10-20 m. The origin of the depression of Laguna Carimagua-Bosque is a drainage system that is

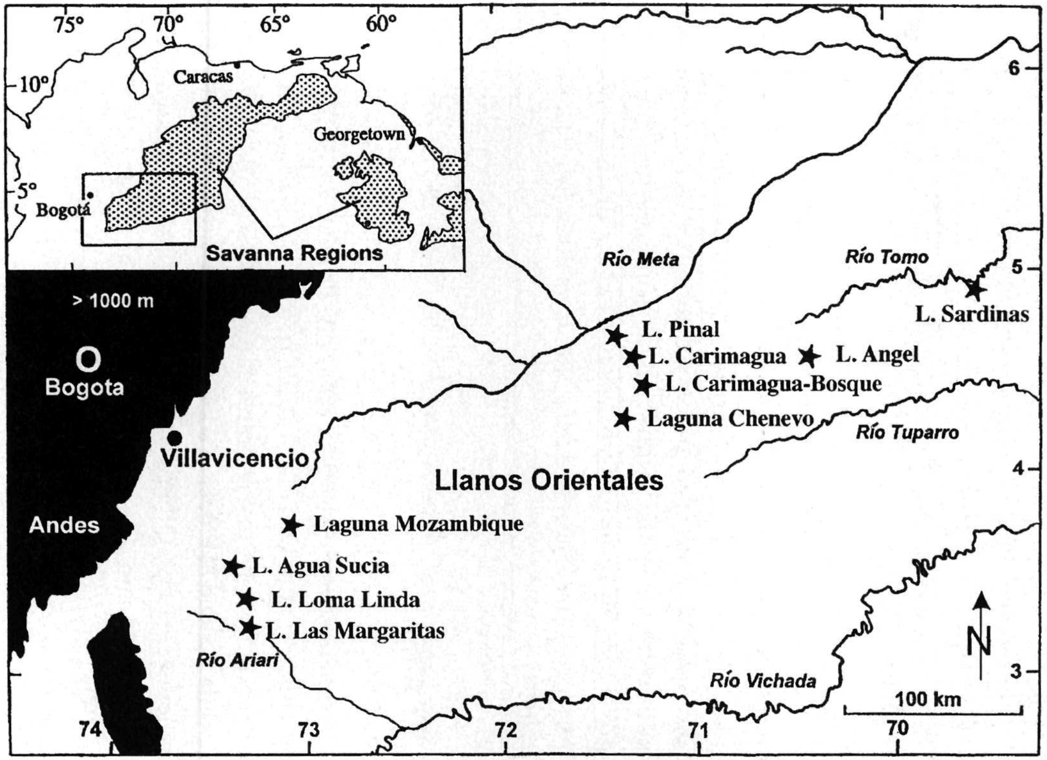

Figure 4.1. Map showing the geographical location of sites Laguna Carimagua and Carimagua-Bosque in the Llanos Orientales of Colombia. Other pollen sites mentionaed in the text are also indicated on the map.

FIGURE 4.2. Photograph of Laguna Carimagua-Bosque (Photo: H. Hooghiemstra)

still present in the area but only active today at some distance. At the shores of Laguna Carimagua an agricultural research station is located called 'Centro de Investigaciones para la Altillanura, Carimagua'.

The climate of the Llanos Orientales is seasonal with a rainy period between April and October (Lowy and Rangel, 1993). In the Llanos Orientales there is a precipitation gradient from 1200-2000 mm/yr in the northern region near the Venezuelan border, to about 2000-2500 mm/yr in the southern and southwestern parts of the savanna area. Based on the records of the Carimagua Reseach Station the local mean annual precipitation is 1860 mm. Mean annual temperature in the study area is 26-27°C with less than 3°C variation between monthly means.

The floral composition of the Colombian savannas was studied by Blydenstein (1967), Huber (1987), Cuatrecasas (1989), and Pinto-Escobar (1993). According to Rangel *et al.*, (1995) the study area is characterised by 'bosque tipo morichal' and as main taxa are mentioned *Mauritia flexuosa, Hedyosmum bonplandianum, Trichantera gigantea, Miconia scorpioides, Caraipa llanorum, Alchornea triplinervia,* and species belonging to the genera *Protium, Vochysia,* and *Cecropia. Hedyosmum bonplandianum* is of special interest as this genus is in palynological studies often regarded as a montane tree. However, these shrubs or small trees occur in Colombia at elevations of 100-2350 m in open habitats along stream edges, ravines, and cleared slopes, as well as in wet montane forest (Todzia, 1988).

Soils in the surrounding area are called 'soils of the esteros', characterised by a fine to medium texture, with moderately high organic matter, and a very poor drainage capacity (Goosen, 1971). The same author pointed out that soils from Carimagua area are structurally weak and that water infiltrating the soils causes translocation of mineral particles.

4.3 METHODS

A modified Livinstone piston corer collected the 65-cm long core Carimagua-Bosque from a wooden platform, which was fixed on two inflatable rubber boats. The core was transported to the Hugo de Vries Laboratory and stored in a cold room (4°C) before sediment samples were collected. For pollen analysis, samples of 1 cm^3 were taken at 2.5-cm intervals along the core. Prior to processing, one tablet of exotic *Lycopodium* spores was added to each sample for calculation of the pollen concentration and pollen influx values. All samples were prepared using the standard pretreatment techniques including sodium pyrophosphate, acetolysis, and heavy liquid separation by bromoform (Faegri *et al.*, 1989). Pollen samples were mounted in a glycerin-gelatin medium. A minimum of 300 pollen grains from terrestrial taxa was counted. Carbonised particles were not counted because during the heavy liquid separation many charcoal particles are eliminated. Pollen identification was based on morphological descriptions by Absy (1979), Hooghiemstra (1984), Roubick and Moreno (1991), Behling (1993), Herrera and Urrego (1996), and the modern reference collection of pollen and spores at the Hugo de Vries Laboratory. Accelerator mass spectrometry (AMS ^{14}C) of 6 bulk samples followed by 3 additional samples of selected plant material were dated at the Van der Graaff Laboratory, University of Utrecht (Van der Borg *et al.*, 1987).

Pollen grains were classified into ecological groups following previous palynological studies of this area (Behling and Hooghiemstra, 1998; Behling and Hooghiemstra, 1999): (1) forest, gallery forest, shrubs and trees; (2) savanna shrubs and trees; (3) savanna herbs; (4) Andean forest taxa; (5) aquatics; (6) unknown; (7) fern spores; (8) fungal spores; (9) *Botryococcus*, and (10) other algal remains. The pollen and spore data are presented as a percentage of the pollen sum, consisting of the groups 1 to 4 that represent the regional vegetation elements and are in competition with each other. For calculation of the pollen and spore frequencies, graphing of the pollen diagrams, and cluster analysis, the software TILIA, TILIAGRAPH, and CONISS were used (Grimm, 1987). The pollen diagrams include individual records of the most important pollen and spore taxa (Fig. 4.3), as well as records of the sums of the ecological groups, downcore changes of the pollen concentration and pollen influx values, and a cluster analysis dendrogram used for zonation (Fig. 4.4).

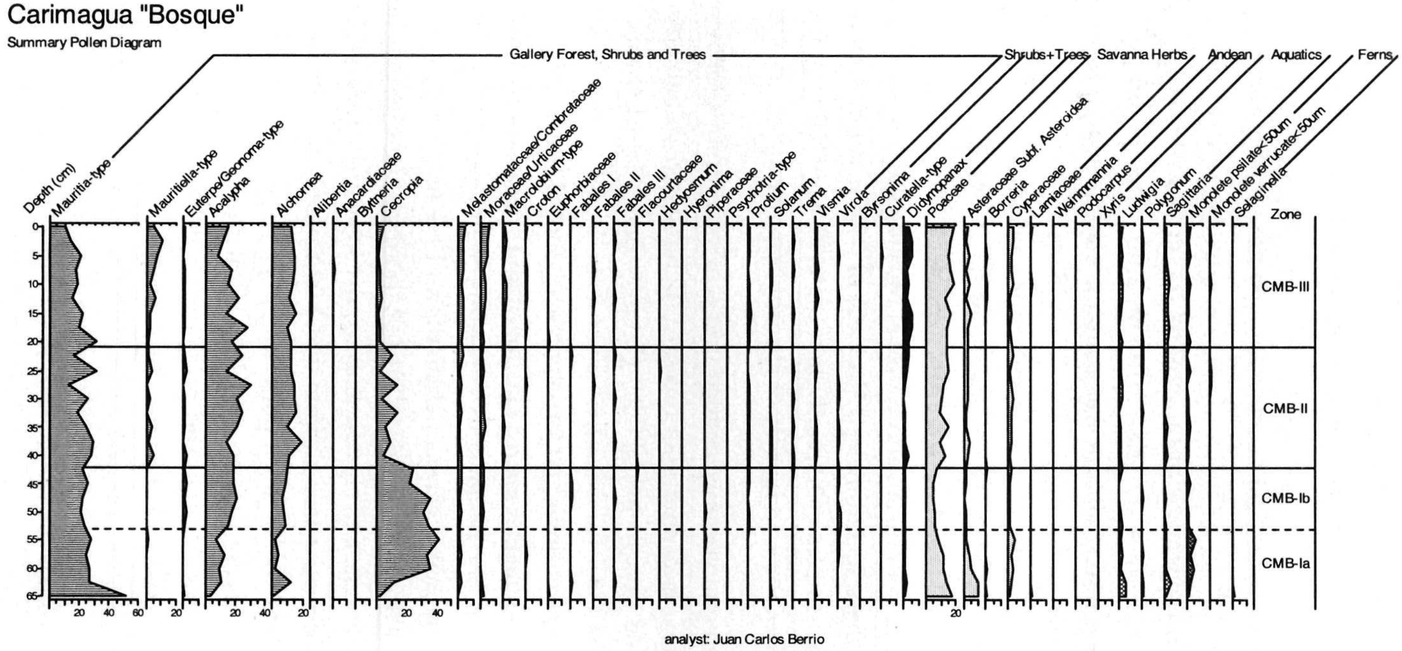

FIGURE 4.3. Percentage pollen diagram of 65-cm core Laguna Carimagua-Bosque, located at 180 m altitude in the Llanos Orientales of Colombia. A selection of the most frequent individual taxa, arranged into ecological groups, is shown.

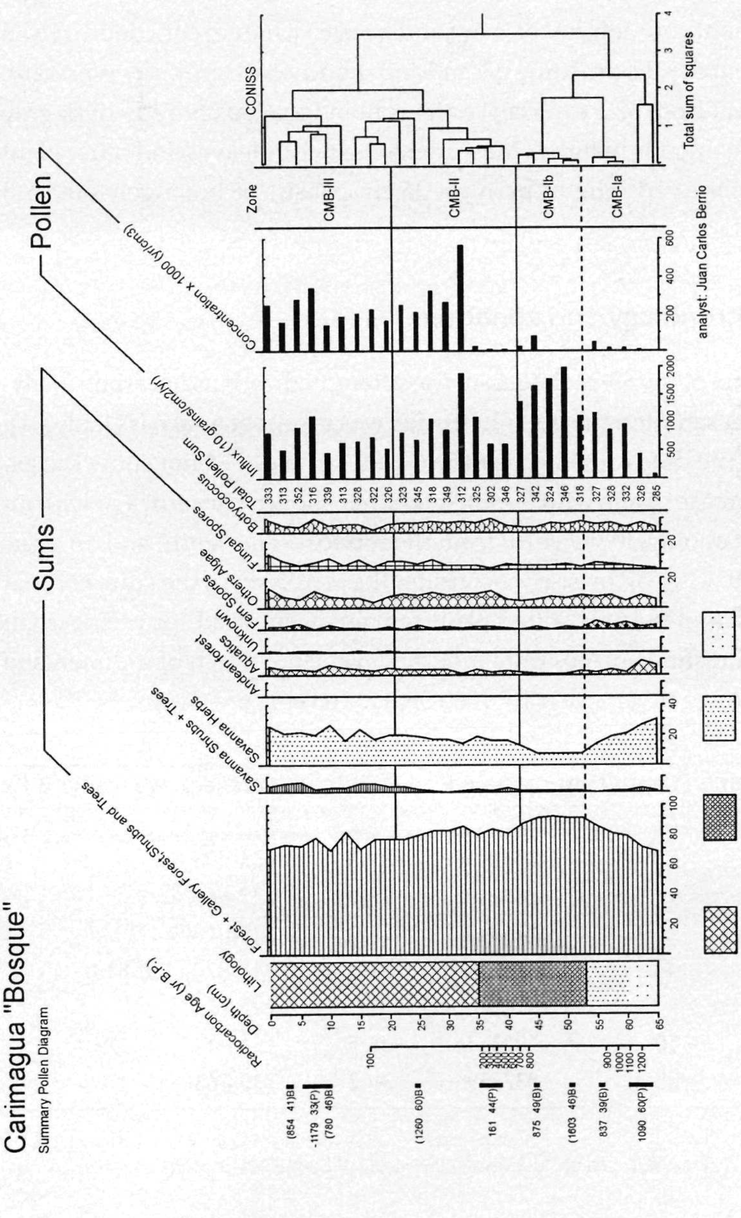

FIGURA 4.4. Summary pollen diagram (sums of ecological groups) of 65 cm core Laguna Carimagua-Bosque, located at 180 m altitude in the Llanos Orientales of Colombia.

4.4 RESULTS

4.4.1. Stratigraphy of the Carimagua "Bosque" Core

The sediment core consists of grey sand from 65 to 60 cm core depth. From 60 to 52.5 cm depths a mixture of sand and muddy dark grey clay is present. The interval from 52.5 to 35 cm contains homogeneous muddy dark grey clay, rich in organic material. Macroremains such as leaves and other plant debris is observed. The uppermost 35 cm consist of homogeneous and compact dark grey clay.

4.4.2. Chronology and zonation

Time control of the 65-cm long core was attempted with radiocarbon analysis of 6 bulk samples; the organic residue was taken for analysis (Table 4.1). However, the dates obtained for the 6 bulk samples did not show the expected increase of age with depth, but rather show a constant age with an average of about 940 ^{14}C yr BP from the top to 45 cm depth, and an average of 1030 ^{14}C yr BP in case we consider the top 55 cm of the core. For that reason 3 samples of identified plant remains were used for radiocarbon analysis and showed ages from modern for the top 40 cm of sediments to 1090±60 ^{14}C yr BP (= cal yr BP 1060-930) for 60 cm core depth.

Lab. Number	Depth (cm)	^{14}C yr B.P.	$^{13}C/^{12}C$ r.	Calendar age (cal yr B.P)
UtC-8008	2.5	854±41	-27.6	784-703
UtC-8009	9	780± 46	-27.8	723-664
UtC-8034	24	1260± 60	-28.2	1270-1077
UtC-8010	44	875±49	-29.9	891-870, 826-814, 792-723
UtC-8011	50	1063±46	-28.5	1535-1411.
UtC-8012	55	837±39	-30.2	770-763

Table 4.1. List of ^{14}C AMS samples dates of Carimagua "Bosque"

Obviously, the ages obtained for the bulk samples do not show a distinct time marker, but rather the age of a carbon fraction, which seems to have penetrated the whole core. The ages of the plant remains show a rapid increase of age between 35 and 65 cm, which corresponds, to a low sediment accumulation rate during this period. The low pollen concentration values in this interval (Fig. 4.3) support this interpretation. There is no indication from the pollen diagram, or from the observed changes that a hiatus is present.

We discuss here some aspects relevant to the problems in the chronology. Goosen (1971) reports soil instability as an important characteristic of this area, allowing the transport of mineralogical soils particles: organic material of a narrow age range could have vertically migrated through the soil column. However in such a case also pollen grains might have migrated vertically. However, the vegetation changes illustrated in the pollen diagram show a plausible development, also when compared to other pollen records from the Llanos Orientales. Therefore, vertical migration of pollen grains is very unlikely. If migration of only mineralogical soil particles is possible remains doubtful. A second explanation is that the total sediment sequence has been deposited in very short time around 800-850 ^{14}C yr BP and that the ages on bulk material at 24 cm and 50 cm core depth are for some reason too old. But for the same reason as given for the first hypothesis this is very unlikely.

Notwithstanding the uncertainty in the time control, we conclude that this core represents vegetation conditions of the latest Holocene. For this reason comparison of the vegetation development shown by core Carimagua-Bosque may be compared to the uppermost parts of the cores Carimagua, El Piñal, and Sardinas, which reflect the same time interval.

In conclusion, we accepted the ages at 5-9 cm, 35-39 cm, 44 cm, 55 cm, and 60-64 cm to calculate the age of the periods represented by the pollen zones. We rejected the samples at 2.5 cm, 9 cm, 24 cm, and 50 cm (these ages are between brackets in Fig. 4.3). The pollen zones, based on significant changes in representation and/or changes in the composition of the pollen spectra, represent the following periods: zone CMB-Ia: 1300 to 875 ^{14}C yr BP, CMB-Ib: 875 to 700 ^{14}C yr BP, zone CMB-II 700 to 125 ^{14}C yr BP, and zone CMB-III 125 ^{14}C yr BP to recent.

4.4.3. Description of the pollen diagram

Zone CMB-Ia (65-53 cm) is characterised by a high representation of pollen of *Mauritia*-type (51%) at the base of the zone. Other important taxa are *Acalypha* and *Alchornea* (5-15%), and *Cecropia* reach its maximum values (45%) at the end of the zone. Melastomataceae/Combretaceae, Moraceae/Urticaceae, and Fabales-I reach only 2%. Savanna shrubs and trees are poorly represented but *Didymopanax* is present with 2%. Savanna herbs are common and maximally represented with 18% Poaceae, 10% Asteraceae, and 5% Cyperaceae. Aquatics reach 5-10%.

At the beginning of zone CMB-Ib (53-42 cm) pollen grains of *Euterpe/Geonoma*-type start to be frequent (2%). *Mauritia*-type (21%), *Acalypha* (22%), *Alchornea* (18%), and *Cecropia* (25-35%) are the most important taxa of the gallery forest. *Byrsonima* and *Didymopanax* are poorly represented in this zone. Savanna herbs decreased and are mainly represented by Poaceae (5-8%), Asteraceae (1%), and Cyperaceae (1%). Aquatics, such as *Ludwigia, Polygonum* and *Sagittaria* show values <1%.

In zone CMB-II (42-21 cm) the contribution of the ecological groups of forest, gallery forest, and shrubs and trees decrease slowly to 78-87%, whereas savanna herbs increase gradually. The record of *Mauritia*-type pollen continues with values similar to the previous zone, but in the uppermost part values varies from 15 to 33%. *Mauritiella*-type pollen starts to be present with 4% in this zone. *Acalypha* is present with 14-28% in this zone. *Alchornea* shows a stable contribution of 18%. Compared to the previous zone *Cecropia* decreases markedly to 2-11%. Melastomataceae/Combretaceae, and Moraceae/Urticaceae show constantly 2%. *Didymopanax* is poorly represented but rises at the uppermost part to 4%. The savanna herbs Poaceae (15%), Asteraceae (4%), and Cyperaceae (5%) show similar values as in zone CMB-Ia. Aquatics increase from 3 to 6%.

In zone CMB-III (21-0 cm) gallery forest continues to decrease to reach 77-65%, *Mauritia*-type decreases to 10%, and *Euterpe/Geonoma*-type to 1%. Compared to the previous zone *Cecropia* is poorly represented (3%). Melastomataceae/Combretaceae, Moraceae/Urticaceae, and *Macrolobium*-type show a stable representation. Less frequent taxa are *Vismia* (3%), and

Croton, Fabales II, *Psychotria*, and *Protium* (all 1-2%). Savanna shrubs and trees (mainly *Didymopanax*) show the highest representation in this zone (7%). Savanna herbs rise again to higher percentages (30%) in the uppermost part of the zone: Poaceae (20%), Asteraceae (5%), and Cyperaceae (4%). Other savanna herbs, such as *Borreria*, Lamiaceae, and *Spermacoce* have 1% as a maximum. Aquatics are continuously represented by *Ludwigia* and *Sagittaria* (2-3%), and by *Xyris* and *Polygonum* (maximally 1.5%).

4.5 ENVIRONMENTAL DEVELOPMENT BASED ON CARIMAGUA-BOSQUE RECORD

Lake Carimagua-Bosque came into existence during the late Holocene and the lake sediments document the development of the dynamic balance between open savanna and gallery forest during the last 1300 ^{14}C yr BP. The interval with sand, gradually changing to sandy clay (65-52.5 cm) dated from 1300-850 ^{14}C yr BP (extrapolated ages) reflects the initial phase of the lake, which possibly developed from an abandoned meander. The drainage system possibly included swampy areas where *Mauritia*-dominated swamp forest ('morichal') was common as reflected by the high representation of this palm pollen. The forest development started with *Cecropia*, a common coloniser, whereas the trees *Acalypha* and *Alchornea* became more frequent in the later part of this initial 450-year long period. Light demanding ferns represented by the records of 'monolete psilate spores' are common in the understory of pioneer forests. While local gallery forest taxa increased, the Poaceae and Asteraceae taxa decreased documenting a reduction in open savanna. Aquatic taxa, such as *Xyris*, *Ludwigia*, and *Sagittaria* were common from the start of the record. Also the presence of the alga *Botryococcus* indicates that stagnant and shallow water was present from the start of the record.

During the period from 875 to 700 ^{14}C yr BP (zone CMB-Ib) the lake was apparently completely surrounded by gallery forest and possibly there was no direct contact any more with the open savanna in the surroundings, as evidenced by the low contribution of the two groups of savanna taxa. Also the lithological column shows that (aeolian) supply of sandy material to the lake had ceased probably prevented by dense forest. The lake started to accumulate dark clay rich in organic material. A significant contributor to the local production of organic material might have been the swamp forest with *Cecropia* and *Mauritiella* growing in the shallow parts of the lake. Pioneer forest of *Cecropia* experienced its maximum extension and was becoming gradually replaced by 'mature' forest mainly consisting of *Acalypha, Alchornea, Euterpe/Geonoma,* Moraceae/Urticaceae, Piperaceae, and *Virola.* Pollen influx values reach the highest values of the total record indicating that the transition from open pioneer forest to more closed gallery forest are favourable conditions for the lake to collect a maximum of pollen.

During the period from 700 to 125 ^{14}C yr BP (zone CMB-II) forest development reached a third phase in which the pioneer tree taxon *Cecropia* lost its dominant role, and *Mauritiella* palms became a new arboreal taxon competing with forest trees. The slightly undulating landscape surrounding the lake was now covered by different vegetation types: (a) swamp forest dominated by *Mauritia* and *Mauritiella* on poorly drained soils, (b) gallery forest dominated by *Acalypha, Alchornea,* and to a lesser degree Anacardiaceae, and *Macrolobium* (on better drained soils), with the light demanding tree taxon *Cecropia* as an indicator for internal forest dynamics and possibly also reflecting *Cecropia* stands at larger distance where the development of the forest may have been at a different stage, (c) elements of the understory partly reflected in the records of the Melastomataceae/Combretaceae, and Moraceae/Urticaceae, (d) savanna shrubs mainly *Didymopanax* and less frequent *Byrsonima,* and (e) savanna herbs dominated by Poaceae.

The youngest part of the reconstruction deals with the period of the last 125 ^{14}C years (zone CMB-III). Although the last decades are probably not represented as the upper most few centimetres of unconsolidated sediments were lost during the coring. The pollen record reflects gallery forest dominated by *Acalypha,* and *Alchornea,* with (partly in the understory) Melastomataceae/Combretaceae, Moraceae/Urticaceae, *Macrolobium, Croton,* Fabales, *Psychotria*-type, *Protium, Vismia,* Anacardiaceae, and *Alibertia. Cecropia* is part of the gallery forest. In the swamp forest *Mauritiella* became common and may have partly replaced *Mauritia*. In the savanna woody taxa, primarily *Didymopanax*, became more frequent. Human impact may have contributed to this change, including the increase of *Mauritiella*, which is frequently used by man. Conditions were wetter during this period on the average. Aquatic vegetation never became important which must be related to the topography of the lake; because the lakeshores are narrow once they are surrounded by forest there is not much shallow area for extensive aquatic vegetation.

4.6. COMPARISON OF SAVANNA POLLEN RECORDS: IMPLICATIONS FOR SAVANNA RECONSTRUCTIONS

Increased percentages of *Cecropia* recorded at Carimagua-Bosque can be interpreted as evidence of increased human impact as suggested also for the Laguna Carimagua record (Fig. 4.5). This suggests that either parts of the drainage system nearby are still changing their routes and continue to provide virgin soil to be colonised by *Cecropia* forest, or that there is disturbance of the vegetation by fire.

In the following section we compare arboreal vs. savanna pollen percentages in four pollen records of the Llanos Orientales that include the last 1500 years. During this period the arboreal vs. savanna pollen ratio within the records show minimal fluctuations in comparison to the difference of this ratio between the cores. Based on these stable ratios in the youngest parts of the pollen records we consider the present-day setting as representative.

(1) pollen record of Laguna Carimagua-Bosque today 100% surrounded by dense gallery forest; this paper,

(2) pollen record of Laguna Carimagua >50% surrounded by grass savanna; Behling and Hooghiemstra (1999),

(3) pollen record of Laguna Sardinas only surrounded by a narrow zone with relatively open morichal vegetation; Behling and Hooghiemstra, 1998,

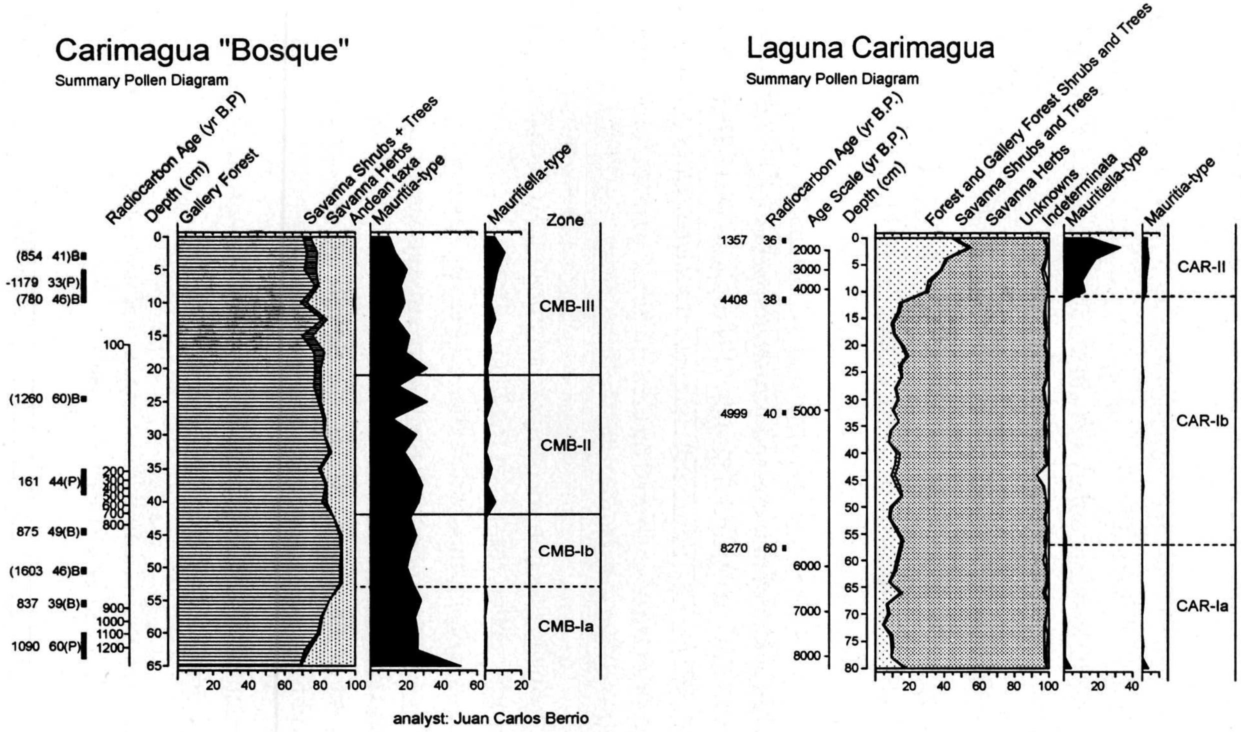

FIGURE 4.5. Comparison of main pollen percentage diagrams of Laguna Carimagua (period of 8000-1350 ^{14}C yr BP, Behling and Hooghiemstra, 1999) and Laguna Carimagua-Bosque (1300 ^{14}C yr BP to recent; this paper). Sites are located ca. 3-km apart at 180-m altitude in the Llanos Orientales of Colombia.

(4) pollen record of Laguna El Piñal surrounded by a narrow zone of very open *Mauritia* palm vegetation, and in fact 100% in contact with the surrounding grass savanna; Behling and Hooghiemstra (1999).

The location of these sites is shown in Fig. 4.1. The records of the lakes Carimagua and Carimagua-Bosque play a special part in this comparison as they are located only some 3 km apart and, considered on a landscape scale, are located in the same drainage system. As shown by the radiocarbon dated pollen records Laguna Carimagua was abandoned in the early Holocene, and Laguna Carimagua-Bosque only in the late Holocene, stressing that the drainage system was dynamic. The Laguna Carimagua record starts at 8270 ^{14}C yr BP and shows a landscape dominated by grass savanna with only a few woody savanna taxa (*Curatella* and *Byrsonima*), and low occurrence of forest and/or gallery forest along the rivers. Up to 3850 ^{14}C yr BP there are only minor changes in the vegetation of the savanna ecosystem. A marked change occurred around the interpolated age of 3850 ^{14}C yr BP, primarily by the sudden high abundance of the palm *Mauritiella*, but also by *Mauritia, Alchornea* and *Cecropia* that became more frequent. This change is related to wetter conditions, i.e. an increase in precipitation and/or a shorter dry season. Behling and Hooghiemstra (1999) tentatively suggested that the increase of the pioneer and disturbance indicator *Cecropia* in the record from Carimagua could be indicative of an increase of human impact on the vegetation after 3850 ^{14}C yr BP. *Mauritiella* today forms dense stands around lake Carimagua which is reflected by the curve of *Mauritiella* in the uppermost part of its record. As suggested by the radiocarbon dates the last thousand years are missing in this record.

In the pollen record from Laguna Carimagua-Bosque (zone CMB-III), the representation of *Mauritia* (10-20%) is higher than of *Mauritiella* (2-10%) and reflects present-day conditions. We conclude that both pollen records do overlap for the period of 1300 to 1000 ^{14}C yr BP which means that zone CMB-Ia (this paper) is coeval with the uppermost part of zone CAR-II (Behling and Hooghiemstra, 1999).

Comparing the ratio arboreal pollen vs. savanna pollen in these four records for the youngest period not older than the last 1300 years, and comparing this ratio in the pollen assemblages with the ratio in the present-day vegetation surrounding the lakes, there is a significant difference between these sites:

(1) the record of Laguna Carimagua-Bosque, today completely surrounded by dense gallery forest up to c. 2 km distance from the lake, shows the highest percentages of arboreal pollen: 70-90%. This lake is a closed system about 150 m in diameter, 1-2 m deep, and located at 180 m elevation at 4°04'N, 70° 13'W.

(2) the record of Laguna Carimagua, today >50% surrounded by grass savanna and with some patches of forest of several hectare reaching the border of the lake, shows 30-50% arboreal pollen.

This lake is a closed system about 3-km long and 1.5 km wide, 0.8-m deep, and located at 180-m elevation at 4°04'N, 70°14'W.

(3) the record of Laguna Sardinas, today surrounded by a narrow zone of open palm forest (morichal) and shrub up to some 50 to 100 m distance from the border of the lake, shows 60-65% arboreal pollen. This lake is a closed system about 800 m in diameter, 1.1 m deep, and located at 80-m elevation at 4°58'N, 69°28'W.

(4) the record of Laguna El Piñal, surrounded by a c. 50 m wide zone with sparsely distributed *Mauritia* palms, and in fact almost completely surrounded by open grass savanna, shows 7-15% arboreal pollen. This lake is a closed system about 1200-m long and 300 m wide, 0.7-m deep, and located at 180-m elevation at 4°08'N, 70°23'W.

We observe that the contribution of arboreal pollen increases with the density of the forest around the lake. Apparently the more lakes are surrounded by gallery forest, the more pollen spectra from these lake sediments are unable to document savannas in the large surroundings. In this respect it is important to observe that the Laguna Carimagua record shows 45-55% of savanna herb taxa, whereas Laguna Carimagua-Bosque shows only 8-20 (30)%. It is very plausible that this difference is directly related to the difference in environmental setting of both lakes: Laguna Carimagua is surrounded by open savanna with over 50% and grass pollen can easily be supplied to the lake sediments. On the contrary, the presence of gallery forest around Laguna Carimagua-Bosque prevents pollen grains from surrounding savanna vegetation to be included in the lake sediments. This is an important observation as it makes clear that the signal of grass pollen in a record from a savanna ecosystem is masked to a significant degree when gallery forest surrounds the lake. This has important implications as most of the drainage system in a savanna ecosystem is hidden by gallery forest, a fact that can be easily seen from an aircraft and from aerial photographs. As shown in the next paragraph this aspect, which is observed thanks to the fact that we can compare pollen assemblages from two neighbouring lakes in different environmental setting, potentially has significant implications for the interpretation of pollen records from sites where pollen assemblages are mainly supplied by water currents.

4.7. POTENTIAL IMPLICATIONS FOR ICE-AGE HISTORY OF AMAZONIA

In the discussion of the ice-age Amazon the central question is whether present-day rain forest had been replaced significantly by dry forest, deciduous forest, and wooded and open savanna-like vegetation during the last glacial maximum (= LGM) (e.g. Colinvaux, 1996; Colinvaux *et al.*, 1996, 2000; Colinvaux, 1997; Hooghiemstra, 1997; Hooghiemstra and Van der Hammen, 1998; Van der Hammen and Hooghiemstra, 2000). As terrestrial records from the Amazonia are scarce, attention focused on pollen records from Amazon Fan cores in order to reconstruct the large-scale vegetation history of the Amazonian rain forest. Haberle (1997), Hoorn (1997), and Haberle and Maslin (1999), showed that the Amazon Fan pollen spectra did not evidence a significantly increased contribution of savanna taxa during the LGM. Colinvaux and co-authors interpreted this pollen signal as evidence that Amazonian forests were not extensively replaced by the above mentioned drier vegetation types, and thereby contradicted the 'forest refugia' hypothesis (see references mentioned above). According to Hoorn (1997), Hooghiemstra (1997), and Hooghiemstra and Van der Hammen (1998) such pollen curves without any major oscillation reflect redeposited and mixed sediments, originating from many places along the Amazon River, and deposited finally offshore.

Our data show for the first time evidence that the presence of a savanna ecosystem is masked in case gallery forest is present preventing pollen to enter the water body. Today most of the drainage system of a savanna is hidden by gallery forest. As a consequence, we expect significant underrepresentation of the savanna ecosystem in river-transported pollen assemblages, and we add here new evidence to the earlier argumention (Hooghiemstra, 1997) why absence of increased percentages of savanna elements in offshore Amazon Fan cores during the LGM is unsufficient evidence to conclude that at LGM time Amazonian rain forest was not significantly replaced by savanna-like vegetation. Additional pollen records and more systematic studies on the relationship between pollen representation and vegetation cover in Amazonian lowlands are needed to improve the argumentation of both 'schools' of the ice-age Amazon.

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4.9 REFERENCES

Absy, M.L., 1979. *A palynological study of Holocene sediments in the Amazon basin*. PhD thesis, University of Amsterdam, Amsterdam, 1-105.

Beard, J.S., 1953. The savanna vegetation of northern tropical America. *Ecological Monographs* 23: 149-215.

Behling, H., 1993. *Untersuchungen zur spätpleistozänen und holozänen Vegetations- und Klimageschichte der tropischen Küstenwälder und der Araukarienwälder in Santa Catarina (Südbrasilien)*. Dissertationes Botanicae 206, 1-149. J. Cramer, Vaduz.

Behling, H., Hooghiemstra, H., 1998. Late Quaternary palaeoecology and palaeoclimatology from pollen records of the savannas of the Llanos Orientales in Colombia. *Palaeogeography Palaeoclimatology Palaeoecology* 139: 251-267.

Behling, H., Hooghiemstra, H., 1999. Environmental history of the Colombian savannas of the Llanos Orientales since the Last Glacial Maximum from lake records El Piñal and Carimagua. *Journal of Paleolimnology* 21: 461-476.

Behling, H., Hooghiemstra, H., 2001. Neotropical savanna environments in space and time: Late Quaternary interhemispheric comparisons. In: Markgraf, V. (ed.), *Inter-hemispheric climatic linkages (Present and past inter-hemispheric climate linkages in the Americas and their social effects)*. Academic Press. Pp. 307-323.

Behling, H., Hooghiemstra, H. 2000. Holocene Amazon rain forest-savanna dynamics and climatic implications: high resolution pollen record Laguna Loma Linda in eastern Colombia. *Journal of Quaternary Science*, 15: 687-695.

Berrío, J.C., Hooghiemstra, Behling, H., Botero. P., Van der Borg, K., 2002. Late Quaternary savanna history of the Colombian Llanos Orientales from Lagunas Chenevo and Mozambique. *The Holocene*, 12(1): 35-48.

Blydestein, J., 1967. Tropical savanna vegetation of the Llanos of Colombia. *Ecology* 48, 1-15.

Colinvaux, P.A., 1996. Quaternary environmental history and forest diversity in the neotropics. In: Jackson, J.B.C. *et al.* (eds), *Evolution and environment in tropical America.* The University of Chicago Press, Chicago & London, 359-405.

Colinvaux, P.A., 1997. The ice-age Amazon and the problem of diversity. NWO/Huygenslezing, Netherlands Organisation for Scientific Research, The Hague, 7-30.

Colinvaux, P.A., de Oliveira, P.E., Moreno, J.E., Miller, M.C., Bush, M.B., 1996. A long pollen record from lowland Amazonia: forest and cooling in glacial times. *Science* 274: 85-88.

Colinvaux, P.A., De Oliveira, P.E., Bush, M.B., 2000. Amazonian and neotropical plant communities on glacial time-scales: the failure of the aridity and refuge hypotheses. *Quaternary Science Reviews* 19: 141-169.

Cuatrecasas. J., 1989. Aspectos de la vegetación natural de Colombia. *Perez-Arbelaezia* 2: 155-283. Jardín Botánico de Bogotá 'José Celestino Mutis'.

Faegri, K., Kaland, P.E., Krzywinski, K., 1989. *Textbook of pollen a*nalysis, 4th edition. Wiley & Sons, Chichester, 328 pp.

Goosen, D., 1971. *Physiography and soils of the Llanos Orientales, Colom*bia. Publicaties van het Fysisch-Geografisch en Bodemkunding Laboratorium van de Universiteit van Amsterdam 20, 1-200.

Grimm, E.C., 1987. CONISS: A Fortran 77 program for stratigraphically constrained cluster analysis by the method of the incremental sum squares. *Computer Geoscience* 13: 13-35.

Haberle, S., 1997. Upper Quaternary vegetation and climate history of the Amazon basin: correlating marine and terrestrial pollen records. *Proceedings Ocean Drilling Program, Scientific Results* 155: 381-396.

Haberle, S., Maslin, M.A., 1999. Late Quaternary vegetation and climate change in the Amazon basin based on a 50,000 year pollen record from the Amazon Fan, ODP Site 932. *Quaternary Research* 51: 27-38.

Herrera, L.F., Urrego, L.E., 1996. *Atlas de polen de plantas útiles y cultivadas de la Amazonia Colombiana (Pollen atlas of useful and cultivated plants in the Colombian Amazon region).* Estudios en la Amazonia Colombiana XI. Tropenbos-Colombia, Bogotá, 462 pp. (also published in: The Quaternary of Colombia 24, H. Hooghiemstra (ed.), Amsterdam).

Hills, T.L., Randall, E. (eds), 1968. The ecology of the forest-savanna boundary. McGill University, *Savanna Research Series* 13: 1-128.

Hooghiemstra, H., 1984. Vegetational and climatic history of the high plain of Bogotá, Colombia: a continuous record of the last 3.5 million years. *Dissertationes Botanicae* 79, 1-368. J. Cramer, Vaduz. (Also published in: The Quaternary of Colombia 10 (ed. T. van der Hammen), Amsterdam).

Hooghiemstra, H., 1997. *Tropical rain forest versus savanna: two sides of a precious medal?* A comment. NWO/Huygenslezing, Netherlands Organisation for Scientific Research, The Hague, 31-43.

Hooghiemstra, H., Van der Hammen, T., 1998. Neogene and Quaternary development of the neotropical rain forest: the forest refugia hypothesis, and a literature overview. *Earth-Science* Reviews 44: 147-183.

Hoorn, C., 1997. Palynology of the Pleistocene glacial/interglacial cycles of the Amazon Fan (Holes 940A, 944A, and 946A). *Proceedings Ocean Drilling Program, Scientific Results* 155: 397-409.

Huber, O., 1987. Neotropical savannas: their flora and vegetation. *Tree* 2: 67-71.

Lowy, P., Rangel, O., 1993. *Caracterización climática de la Orinoquía Colombiana. Contribución del Proyecto Estudio de la Diversidad Biótica de Colombia.* Convenio Inderena-Universidad Nacional de Colombia. (Documento Interno).

Monasterio, M., Sarmiento, G., 1971. Ecología de sabanas de America Tropical. I. Análisis macroecológico de los llanos de Calabozo, Venezuela. *Cuadernos Geográficos* 4: 1-126.

Pinto-Escobar, P., 1993. *Vegetación y flora de Colombia.* Editorial Guadalupe, Bogotá, 72 pp.

Rangel, J.O., Sánchez, H., Lowy, P., Aguilar, M., Castillo, A., 1995. Region de la Orinoquia. In: Rangel, J.O. (ed.), *Colombia diversidad biotica I.* Instituto de Ciencias Naturales, Universidad Nacional de Colombia, 239-254.

Roubick, D.W., Moreno, J.E., 1991. *Pollen and spores of Barro Colorado Island.* Missouri Botanical Garden 36, 270 pp.

Rull, V., 1992. Successional patterns of the Gran Sabana (southeastern Venezuela) vegetation during the last 5000 years, and its responses to climatic fluctuations and fire. *Journal of Biogeography* 19: 329-338.

Rull, V., 1999. A palynological record of a secondary succession after fire in the Gran Sabana, Venezuela. *Journal of Quaternary Science* 14: 137-152.

Sarmiento, G., Monasterio, M., 1975. A critical consideration of the environmental conditions associated with the occurrence of savanna ecosystems in tropical America. In: Golley, F.B., Medina, E. (eds), *Tropical ecological systems; trends in terrestrial and aquatic research.* Springer, Berlin, 223-250.

Todzia, C.A., 1988. *Flora Neotropica, 48. Chloranthaceae: Hedyosmum,*. The New York Botanical Garden, New York, 139 pp.

Van der Borg, K., Alderliesten, A., Harnton, C.M, De Jong, A.F., Van Zwol, N.A., 1987. Accelerator mass spectrometry with ^{14}C and ^{10}Be in Utrecht. *Nuclear Instruments Methods B29*: 143-145

Van der Hammen, T., 1983. The palaeoecology and palaeogeography of savannas. *In*: Bourliere, F. (ed.), *Tropical savannas. Ecosystems of the World* 13: 19-35. Elsevier, Amsterdam.

Van der Hammen, T. Hooghiemstra, H., 2000. Neogene and Quaternary history of vegetation, climate, and plant diversity in Amazonia. *Quaternary Science Reviews* 15: 725-742.

Wijmstra, T.A., 1971. *Palynology of Guiana coastal basin.* PhD thesis, University of Amsterdam. 63 pp.

Wijmstra, T.A., Van der Hammen, T., 1966. Palynological data on the history of tropical savannas in the northern South America. *Leidse Geologische Mededelingen* 38: 71-90.

Wille, M., Behling, H., Hooghiemstra, H., Submitted. Vegetation history in the western savannas of the Llanos Orientales of Colombia, based on a 8200-yr pollen record from Laguna Las Margaritas. *Palaeogeography Palaeoclimatology Palaeoecology*