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# Holocene Amazon rainforest–savanna dynamics and climatic implications: high-resolution pollen record from Laguna Loma Linda in eastern Colombia

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ABSTRACT: We present a high-resolution pollen record of a 695-cm-long sediment core from Laguna Loma Linda, located at an altitude of 310 m in the transitional zone between the savannas of the Llanos Orientales and the Amazonian rainforest, about 100 km from the Eastern Cordillera. Based on eight AMS $^{14}$C ages, the record represents the last 8700 $^{14}$C yr BP. During the period from 8700 to 6000 $^{14}$C yr BP the vegetation was dominated by grass savanna with only a few woody taxa, such as *Curatella* and *Byrsonima*, present in low abundance. Gallery forest along the drainage system apparently was poorly developed. Compared with today, precipitation must have been significantly lower and seasonality stronger. During the period from 6000 to 3600 $^{14}$C yr BP, rainforest taxa increased markedly, reflecting an increase in precipitation. Rainforest and gallery forest taxa such as Moraceae/Urticaceae, Melastomataceae, *Alchornea, Cecropia* and *Acalypha*, were abundant, whereas Poaceae were reduced in frequency. From 3600 to 2300 $^{14}$C yr BP rainforest taxa continued to increase; Moraceae/Urticaceae became very frequent, and Myrtaceae and *Myrsine* became common. Savanna vegetation decreased continuously. We infer that precipitation was still increasing, and that the length of the annual dry period possibly shortened. From 2300 $^{14}$C yr BP onwards, grass savanna (mainly represented by Poaceae) expanded and *Mauritia* palms became frequent. This reflects increased human impact on the vegetation. Copyright © 2000 John Wiley & Sons, Ltd.

KEYWORDS: Amazonian rainforest; savanna; vegetation dynamics; climate dynamics; Holocene; human impact; Colombia.

## Introduction

The Late Quaternary environmental history of the tropical lowland ecosystems in the neotropics is poorly known despite the importance of understanding the natural amplitude of tropical ecosystem dynamics, which would help to verify global climate models and to better understand global biodiversity in relation to ecosystem dynamics. The lowlands of eastern Colombia are characterised by a strong gradient in precipitation and seasonality, which is reflected in the vegetation zonation: the savannas to the north gradually change into a large area of rainforest to the south. The late Quaternary history of both ecosystems is still poorly known. This explains the ongoing discussion in the literature about the degree to which rainforest and savanna replace each other when climatic conditions change (e.g. Van der Hammen and Absy, 1994; Colinvaux *et al*., 1996; Hooghiemstra and Van der Hammen, 1998; Van der Hammen and Hooghiemstra, 2000).

The Late Quaternary history of the savannas north of the Amazon basin is known from a number of sites. The first palynological information on the Holocene vegetation history and climatic change of the Llanos Orientales came from Laguna de Agua Sucia (Wijmstra and Van der Hammen, 1966). Other palynological studies from savanna ecosystems of northern South America are available from the Gran Sabana in Venezuela (Rull, 1992), the Rupununi savanna in Surinam (Wijmstra and Van der Hammen, 1966) and the

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belt of coastal Guianan savannas in Surinam (Wijmstra, 1971), British Guyana (Van der Hammen, 1963) and French Guiana (Tissot and Marius, 1992). Recently, the savannas of the Colombian Llanos Orientales were explored by the Hugo de Vries Laboratory of Amsterdam University. Starting from the city of Villavicencio, which is located in the foothills of the Eastern Cordillera, we collected sediment cores in 13 lakes and swamps along a 500 km long transect, running from west to east (Fig. 1). The sites are located between 3°30′ to 4°30′N latitude and 69° to 74°W longitude, at elevations between 80 and 450 m in the provinces of Meta and Vichada. Results from the pollen analysis of cores from Lagunas Angel and Sardinas (Behling and Hooghiemstra, 1998), and Lagunas El Piñal and Carimagua (Behling and Hooghiemstra, 1999) have been published. An overview and comparison of the savanna ecosystems north and south of the Amazonian rainforest has been prepared by Behling and Hooghiemstra (in press).

The Late Quaternary history of the northwestern part of the Amazonian rainforest area is known from only a few sites. In the Colombian part, Van der Hammen *et al.* (1992a, b) studied the middle Caquetá River area, Urrego (1991, 1997) studied pollen records from sites at Mariñame and Quinché representing the complete Holocene, also located along the middle Caquetá River. Behling *et al.* (1999) studied cores from Pantano de Monica, located in the middle Caquetá River area, also representing the complete Holocene. From the Brazilian part of northwest Amazonia, Colinvaux *et al.* (1996) published a Late Quaternary pollen record from Laguna La Pata.

Except for Laguna de Agua Sucia, all sites previously studied are located far from the savanna–rainforest boundary. The site presented in this paper, Laguna Loma Linda, is located in the present-day transition between savanna and rainforest and, as a consequence, is sensitive for registering changes between both types. The geographical location of the savanna–rainforest boundary depends mainly on climatological factors, i.e. differences in the total annual precipitation and the distribution of rain throughout the year (seasonality); it also depends on other environmental factors, such as biotic, pedological and physical factors (Cole, 1982, 1986; Medina and Silva, 1990).

From the sites mentioned above, the following Late Quaternary vegetation history has been inferred. During the last 18000 $^{14}$C yr BP the savanna ecosystem was relatively stable, except for minor changes in floral composition, and in the proportion of savanna to forest. During the Last Glacial Maximum (LGM) the reduced area of gallery forest and the non-permanent lake conditions (Laguna El Piñal) reflect the driest period of the whole record, probably due to low rainfall rates and a long annual dry season. In this region gallery forest started to expand during the Late-glacial, at around 10700 $^{14}$C yr BP (Laguna El Piñal and Laguna Sardinas), indicating wetter conditions than during the LGM. During the early Holocene, gallery forest diminished compared with the Late-glacial, reflecting markedly drier conditions again, but not as dry as the LGM. Starting at 6400 $^{14}$C yr BP (Laguna Sardinas), and at 5300 $^{14}$C yr BP (Laguna Angel), gallery forests expanded, suggesting a change to wetter conditions. The marked increase of palms (*Mauritia* and *Mauritiella*) during the last ca. 3500 $^{14}$C yr BP in most of the sites of the Llanos Orientales, points to increased human impact on the vegetation under the wettest climate regime registered in the Holocene.

The pollen records from the middle Caquetá River area show that during the Late-glacial and early Holocene the lower terraces were better drained than during the last 4000 yr. Observed changes are the result of changes in the drainage system of the Caquetá River basin. These changes might be either the consequence of river dynamics in the valley of the Rio Caquetá, or of climate change, i.e. less precipitation and reduced river discharge.

The objective of this paper is to document in detail the dynamics between savanna and rainforest during the Holocene from the Amazon lowlands and to infer a record of climatic change. The effects of possible human impact on both ecosystems are evaluated.

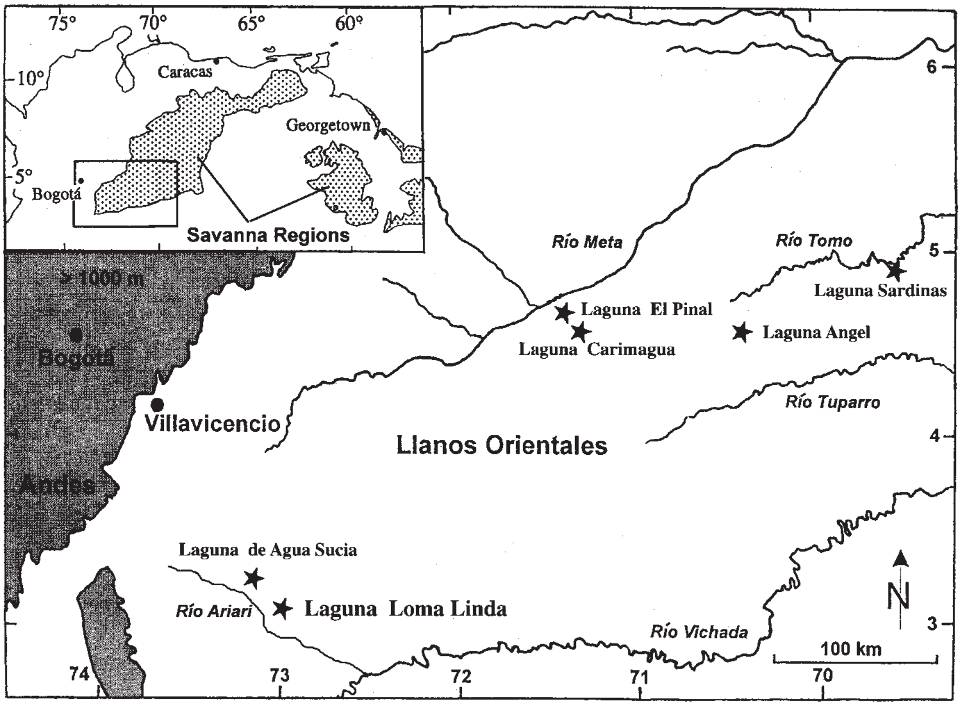


**Figure 1** Map showing the geographical location of the site studied, Laguna Loma Linda, and the sites mentioned in the text, Laguna Angel and Laguna Sardinas, Laguna El Pinal, Laguna Carimagua and Laguna Agua Sucia.

 

## Environmental setting of the study area

Laguna Loma Linda (3°18′N, 73°23′W) is located in the province of Meta, about 120 km southeast of the city Villavicencio. The distance to the Eastern Cordillera is about 100 km. The lake is situated within the borders of a military area, some 10 km north of the town of Puerto Lleras, in a soft rolling landscape at 310 m elevation (Fig. 2). The lake is about 2.5 km long and 1 km wide, and was part of a former small river which became dammed probably at the beginning of the Holocene. The lake is isolated and apparently has no connections to other rivers. The water depth of the lake was 280 cm during coring on 14 February 1996.

### Vegetation

The modern vegetation of the study area, located in the contact zone between the savanna of the Llanos Orientales and the Amazonian rainforest, is significantly influenced by human activity. Large areas have been transformed into pasture land. A few patches of probable secondary forest and stands of the palm *Mauritia* (local name 'morichi') occur in the surroundings of the lake. The savannas of the Llanos Orientales are characterised mainly by the different types of herbaceous savannas with shrubs and shrubby trees, and gallery forest along the rivers (Chaves and Arango, 1998). Botero (1999) published an extensive study on the geomorphology, vegetation, and climate of the eastern Colombian lowlands between the Venezuelan and Brazilian borders. At some places between the rivers, patches of forest occur where the plant composition is comparable to Amazonian forest. General data on the flora and ecology of the savannas of the Llanos was published by Cuatrecasas (1989), Gentry (1993), Huber (1987), Hueck (1966), Hueck and Seibert (1972), Pinto-Escobar (1993) and Vareschi (1980). Blydenstein (1967) recognised 10 different plant associations in the savannas of the Llanos Orientales. Along water courses, including lake borders and swampy areas, often dense stands of the palm *Mauritia* are found. *Mauritia* swamp forest is called 'morichal'. The smaller palm *Mauritiella* grows along lake shores in shallow water and surrounds several lakes in the Llanos Orientales.

The forest of Colombian Amazonia is a dense and tall and highly diverse rainforest. A detailed vegetation survey and mapping of the middle Caquetá region has been published by Duivenvoorden and Lips (1993, 1995), Urrego (1991, 1997) and Botero (1999), who has published vegetation and geomorphological maps of the total lowlands of eastern Colombia.

### Climate

The climate of the Llanos Orientales is strongly seasonal. The marked annual dry period lasts about 4 to 5 months, from mid-November to mid-March. In the province of Arauca to the north, the dry season is longer than in the provinces of Meta and Vichada to the south. The seasonal climate with a rainy and a marked dry period is related to the annual movement of the intertropical convergence zone (ITCZ). Precipitation ranges from 1200–2000 mm $yr^{-1}$ in the north to about 2000–2500 mm $yr^{-1}$ in the southern and southwestern parts of the savanna area. In the zone where savanna is replaced by rainforest the annual precipitation is over 2400–2500 mm $yr^{-1}$ and the annual dry period lasts about 3 months. In the central Amazon region there is no, or only a short, dry period and precipitation is above ca. 3000 mm $yr^{-1}$. Mean annual temperature in the study area is about 26°C (Blydenstein, 1967; Snow, 1976).

## Methods

The sediments were cored in the centre of the lake from a wooden platform fixed on two inflatable rubber boats. We

**Figure 2** Photograph of Laguna Loma Linda, located in the southern savannas of the Llanos Orientales of Colombia. (Photographed by H. Behling.)

 

used a modified Livingstone piston sampler. The recovered core is 5 cm in diameter and 695 cm long. Sediments were kept in the original aluminium tube and transported to the laboratory in Amsterdam. Core material was stored in a dark cold room at 4°C.

Eight small bulk sediment samples were dated by Accelerator Mass Spectrometry (AMS) at the University of Utrecht (Van der Borg *et al.*, 1987). Sediment samples of 0·5 $cm^3$ were taken at 10 cm intervals for pollen analysis. All samples were prepared using the standard chemical pretreatment, including sodium pyrophosphate, acetolysis and heavy liquid separation by bromoform (Faegri and Iversen, 1989). Exotic *Lycopodium* spores were added to each sample before treatment for calculation of pollen concentration and influx values. Pollen samples were mounted in glycerin gelatin and slides were counted at 500 × magnification. Pollen grains in the pollen samples were well preserved, except from samples in the lower core section, which were not included in the pollen diagrams. For identification, pollen morphological descriptions published by Behling (1993), Herrera and Urrego (1996), Hooghiemstra (1984), Roubik and Moreno (1991) and the reference collections at the Hugo de Vries-Laboratory were used. A minimum of 300 pollen grains of terrestrial taxa were counted. Carbonised particles were not counted on the pollen slides as many charcoal particles are eliminated during heavy liquid separation.

Pollen and spore counts are presented as a percentage of the pollen sum, which includes all pollen except for aquatic taxa. Fern spores, moss spores, fungal spores and algae are not included in the pollen sum. Species of Cyperaceae grow frequently in the savanna vegetation and are considered as a part of the regional vegetation; therefore Cyperaceae were included in the pollen sum. The following ecological groups were identified: (i) shrubs and trees of the rainforest and gallery forest, (ii) savanna shrubs and trees, (iii) savanna herbs, (iv) aquatics and (v) ferns. For calculations, data plotting and cluster analysis we used TILIA, TILIAGRAPH and CONISS software (Grimm, 1987). In total 152 pollen and spore types were recognised; 23 types remained unknown. The pollen diagram (Fig. 3) shows records of the most abundant pollen and spore taxa. Figure 4 illustrates records of the ecological groups, records for fungal spores, *Botryococcus, Pediastrum*, total pollen sum, pollen concentration and pollen influx, and a cluster analysis dendrogram.

## Results

### Stratigraphy

The 695-cm-long sediment core from the Loma Linda site consists mainly of fine detritus mud (0–80 cm depth), fine detritus mud with clay (80–175 cm), changing to grey clay with fine detritus mud (175–244 cm) and the lowermost part of the core consists of grey clay (244–695). A detailed description of stratigraphical changes is as follows:

| | |
|---|---|
| 0–80 cm | green/grey soft fine detritus mud, below 24 cm: compact |
| 80–175 cm | light green/grey compact fine detritus mud with clay, a few leaf fragments |
| 175–200 cm | grey clay with fine detritus mud, 175–186 cm: several plant remains |
| 200–244 cm | dark grey clay with fine detritus mud, charcoal fragments |
| 244–408 cm | dark grey clay, many plant remains and charcoal, 283–300 cm: darker and less plant remains, below 300 cm: with vertical rootlets, 388–408 cm: some grey patches |
| 408–415 cm | grey clay with dark green patches, rootlets |
| 415–427 cm | transition to |
| 427–437 cm | dark grey clay with rootlets |
| 437–442 cm | grey clay with rootlets, black layers at 437, 438·5 and 441·5 cm depth |
| 442–449 cm | transition to |
| 449–458 cm | dark grey clay, less rootlets |
| 458–464 cm | transition to |
| 464–469 cm | grey/brown clay, rootlets |
| 469–512 cm | grey clay, rootlets, 474–492 cm: several dark grey layers |
| 512–591 cm | dark grey clay with few plant remains, rootlets at 550 cm depth |
| 591–695 cm | grey clay with plant remains and charcoal, 591–593 cm: fine laminated, 593–609 cm: grey/green clay, 627–633 cm: charcoal layers, 652–681 cm: rootlets, 681–695 cm: grey/brown clay |

### Chronology and pollen zonation

The eight AMS radiocarbon dates listed in Table 1 provide a detailed chronological control of the lake sediments. The AMS date near the base of the core, at 691 cm depth, documents that the lake contains deposits which cover the last 8700 $^{14}C$ yr BP. The series of AMS dates shows a regular down-core increase of age, which indicates that sediments accumulated continuously. Only the last 700 yr are poorly represented. Cluster analysis of terrestrial pollen taxa produces a dendrogram that permits zonation of the core into the following pollen zones: Zone LL-I (695–427 cm, 8720–6060 $^{14}C$ yr BP, 24 samples), Zone LL-II (427–204 cm, 6060–3590 $^{14}C$ yr BP, 22 samples), Zone LL-IIIa (204–104 cm, 3590–2310 $^{14}C$ yr BP, 10 samples), and Zone LL-IIIb (104–0 cm, 2310 $^{14}C$ yr BP – subrecent, 11 samples).

### Concise description of the pollen diagram (Figs 3 and 4)

The pollen diagram of the Loma Linda site (Fig. 3) shows the most abundant pollen and spore taxa out of the 152 types identified, including 23 unknown types. Down-core changes of pollen concentration and pollen influx are relatively stable, except a few single samples with higher values. Carbonised particles, which were not quantified for reasons mentioned above, are abundant in all pollen samples.

Zone LL-I is marked by a high representation of savanna herbs (80–90%), primarily Poaceae (30–80%), Cyperaceae (10–40%) and minor Asteraceae (0–2%). Taxa of forest and gallery forest total 10%, primarily represented by Moraceae/Urticaceae, Melastomataceae, *Alchornea, Cecropia* and *Acalypha*. Savanna shrubs and trees are poorly represented.

Zone LL-II is characterised by a marked increase of forest and gallery forest taxa from 10% in the previous zone to 30–50% in this zone. This group includes taxa such as Moraceae/Urticaceae (10–30%), Melastomataceae (1–3%), *Alchornea* (2–10%), *Cecropia* (1–8%), *Acalypha* (1–3%), *Piper* (0–1%), *Euterpe/Geonoma* type (0–1%) and *Mauritia*

 

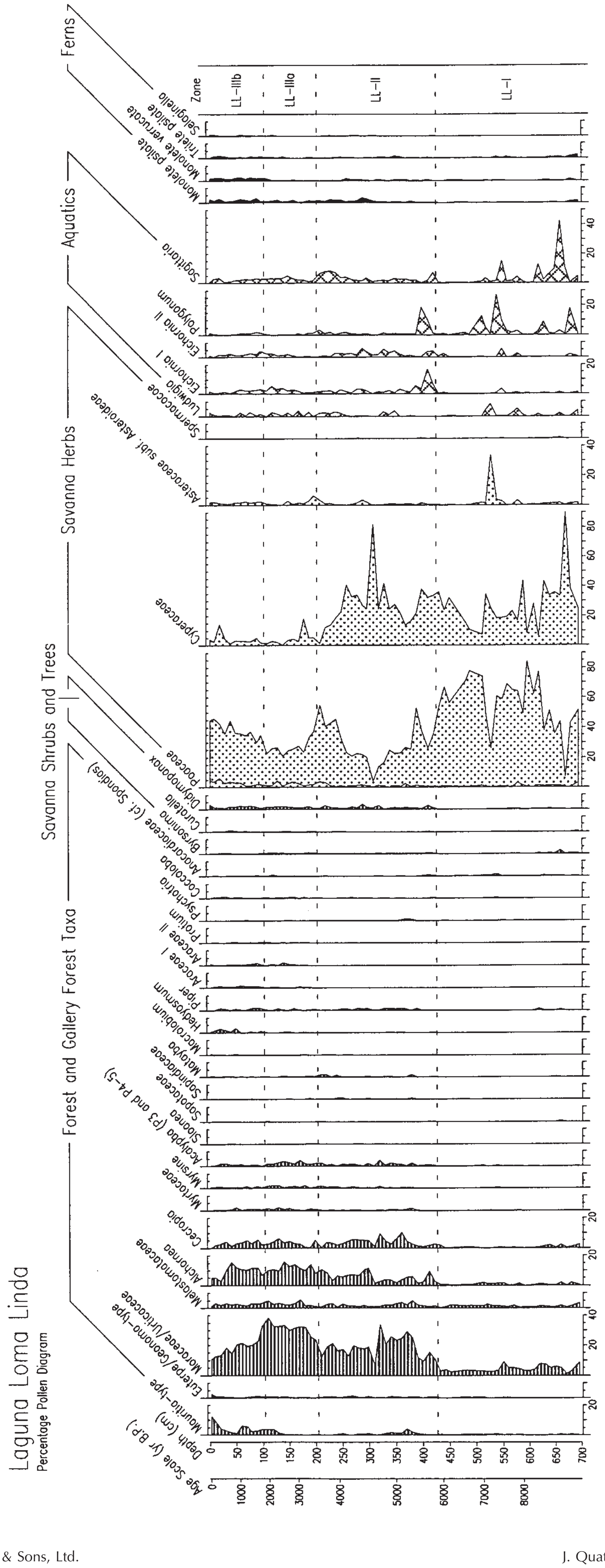


**Figure 3** Pollen percentage diagram of core Laguna Loma Linda, located at 310 m elevation in the southern savannas of the Llanos Orientales of Colombia.

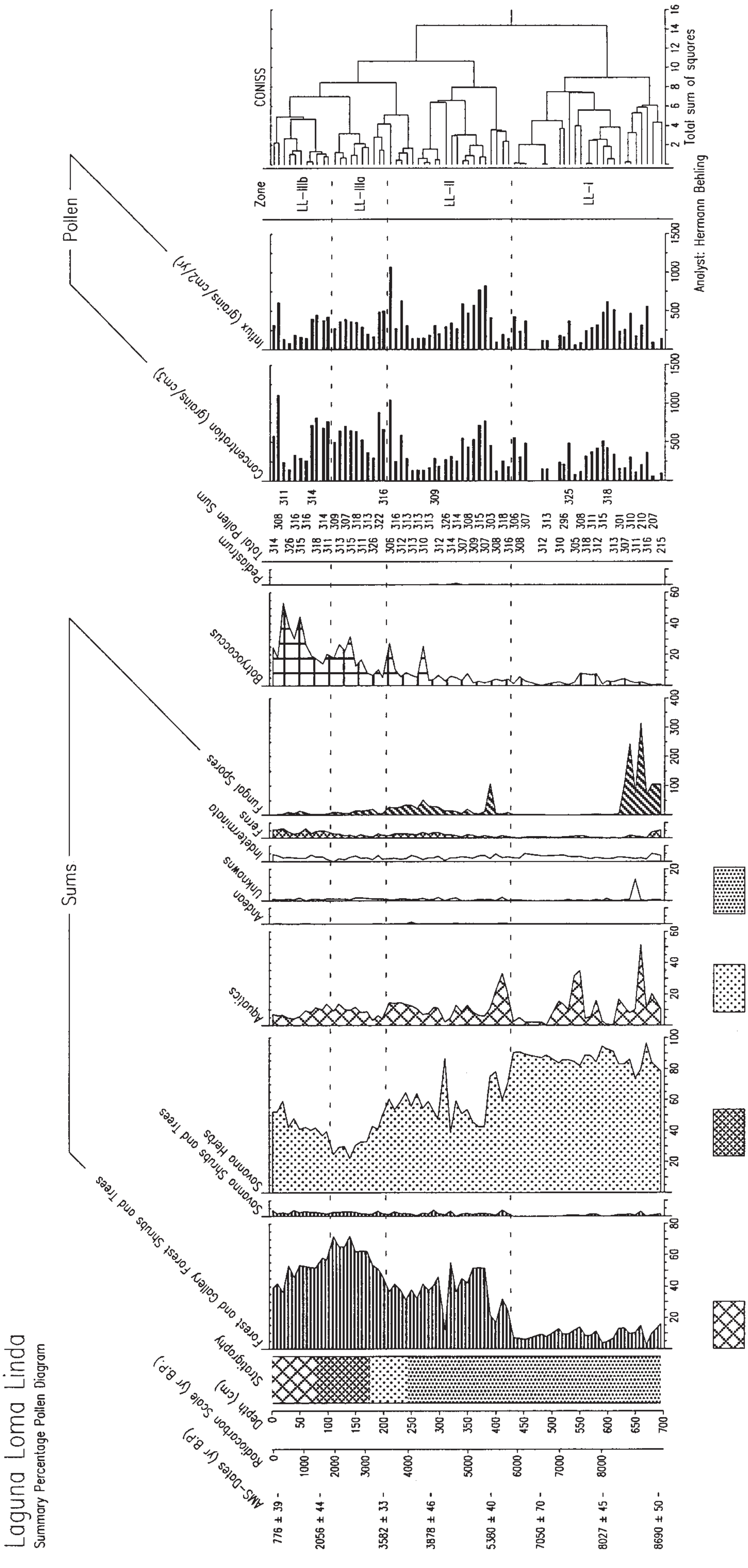


**Figure 4** Pollen percentage diagram of core Laguna Loma Linda showing the sums of ecological groups, records of the pollen concentration and pollen influx, and the cluster analysis dendrogram.

**Table 1** List of AMS radiocarbon dates of samples from the core Laguna Loma Linda

| Laboratory number | Depth (cm) | $^{14}C$ yr BP | $^{13}C/^{12}C$ r. | Calendar age (cal. BC) |
|---|---|---|---|---|
| UtC-6803 | 10 | 776 ± 39 | –27.0 | 718–665 cal. yr BP |
| UtC-6802 | 85 | 2056 ± 44 | –27.9 | 2052–1946 cal. yr BP |
| UtC-5474 | 199 | 3582 ± 33 | –25.8 | 1950–1883 |
| UtC-6801 | 284 | 3878 ± 46 | –28.6 | 4405–4230 cal. yr BP |
| UtC-4964 | 391 | 5380 ± 40 | –26.7 | 4320–4286, 4259–4224, 4189–4158 |
| UtC-6800 | 479 | 7050 ± 70 | –25.6 | 7914–7755 cal. yr BP |
| UtC-5475 | 591 | 8027 ± 45 | –24.9 | 7035–6995, 6955–6941, 6925–6869, 6842–6778 |
| UtC-4965 | 691 | 8690 ± 50 | –26.1 | 7877–7813, 7711–7580 |

(0–3%). Savanna shrubs and trees, such as *Byrsonima, Curatella* and *Didymopanax*, show higher values of 3–5%. Savanna herbs, mainly represented by Poaceae and Cyperaceae, decrease markedly to 60–40%, a decrease that is almost totally caused by a decrease of Poaceae. Ferns are represented from this time on as a continuous curve of 1–4%, aquatics (*Eichornea, Sagittaria*, and less frequent *Polygonum* and *Ludwigia*) show from this zone upwards continuous values of 5–15%, and algae (*Botryococcus*) increase in frequency to 5–20%.

Zone LL-IIIa shows the highest percentages of forest and gallery forest in the record, due mainly to maximum values of Moraceae/Urticaceae (30–35%), *Acalypha* (2–4%), Myrtaceae (2%) and *Myrsine* (2%). At the same time savanna herbs show very low values, due mainly to a sharp decrease in Cyperaceae (2–10% compared with 15–40% in the previous zone). Compared with the previous zone, the contribution of savanna shrubs and trees, aquatics, and ferns do not change, whereas *Botryococcus* increases to 20–30%.

Zone LL-IIIb shows decreasing percentages of forest and gallery forest taxa (from 50–70% in zone IIIa to 40% at the end of this zone); Moraceae/Urticaceae and *Alchornea* especially decrease. Savanna shrubs (*Byrsonima, Curatella* and *Didymopanax*) and trees remain with constant values, but savanna herbs (mainly Poaceae) increase from 30% to 55% at the top of the record. Aquatics decrease slightly from 10% to 5%, but *Botryococcus* shows an increase to about 40%. Ferns also show their highest values in this zone (3–5%).

## Past vegetational and climatic dynamics

During the early Holocene period between 8720 and 6060 $^{14}C$ yr BP (zone LL-I) the pollen spectra document a landscape dominated by grass savanna in which woody savanna shrubs and trees were sparse. Along the drainage system, gallery forests were limited. The savannas of the Colombian Llanos Orientales were at that time much more extensive compared with today and probably reached at least 100 km further to the south. As a consequence, annual precipitation must have been significantly lower, and the length of the annual dry season longer than today. Changes between the different grey colours of the clay deposits in the lowermost part of the core, the presence of roots in the lake deposits and levels with high percentages of Cyperaceae, *Ludwigia*, *Polygonum* and *Sagittaria*, are all indicative of low water levels to allow vegetation to be present in what is now the centre of the lake. Abundant charcoal fragments in the core, also seen in the pollen slides, indicates that the grass savanna burned frequently.

At 6060 $^{14}C$ yr BP, gallery forest expanded significantly, replacing the grass savanna and leading to a new balance between forest and savanna during the period of 6060 to 3590 $^{14}C$ yr BP (zone LL-II). Savanna trees and shrubs also became more frequent. Apparently gallery forest expanded along the drainage system in the valleys, and the remaining grass savanna of the hills ('lomas') became more wooded. The floristic change of the gallery forest, especially the increase in contribution of Moraceae/Urticaceae, *Alchornea* and *Acalypha*, shows that characteristic taxa of Amazonian forest became more frequent in the expanded gallery forest. These changes in vegetation composition indicate that a marked change to wetter conditions took place around 6000 $^{14}C$ yr BP. Increased presence of the disturbance indicator *Cecropia* suggests that fire continued to be common in the savanna.

After this relatively stable period, forest started to expand continuously during the period from 3590 to 2310 $^{14}C$ yr BP (zone LL-IIIa), reducing the area covered by savanna. An increasing expansion of Amazonian rainforest taxa points to increasingly higher precipitation rates.

During the last 2300 $^{14}C$ yr BP (zone LL-IIIb) grass savanna expanded again and stands of palm forest of *Mauritia* ('morichi') developed in the area of Loma Linda, suggesting that human impact increased significantly on the vegetation. The increased presence of *Hedyosmum,* probably *Hedyosmum bonplandianum* (Todzia, 1988), points to increased disturbance and/or to a change to wetter climatic conditions. It is plausible that the area of Loma Linda would have been forested by Amazonian rainforest since 2300 $^{14}C$ yr BP if human impact on the vegetation had been absent.

## Discussion and conclusions

This new high-resolution record supports the general development of vegetation and climate inferred from our previous studies of the Llanos Orientales. The regular and relatively high sediment accumulation in this new core permits a detailed and high-resolution reconstruction of past environmental changes. The almost complete Holocene interval is represented here in 695 cm of sediment, whereas at sites located in the central savanna area the entire Holocene is represented by, for example, 95 cm at Laguna Angel, 65 cm at Laguna Sardinas, 50 cm at Laguna El Pinal, and ca. 80 cm at Laguna Carimagua (Behling and Hooghiemstra, 1998, 1999).

 

The pollen record of the Loma Linda site suggests that the savanna of the Llanos Orientales extended probably at least 100 km further south during the early Holocene period between 8720 and 6060 $^{14}C$ yr BP, reflecting significantly drier climatic conditions compared with today. During the mid-Holocene, a marked increase of gallery forest in the Llanos Orientales is shown in the record of Laguna Angel at 5260 $^{14}C$ yr BP, and at 6390 $^{14}C$ yr BP at the site of Laguna Sardinas. The initial phase of this change from early Holocene dry to mid-Holocene wetter conditions is now best documented at 6060 $^{14}C$ yr BP in the pollen record of Laguna Loma Linda. We conclude that records from the savanna-rainforest transition are more sensitive for vegetational and climatic change than records from sites located in the central parts of the savanna or rainforest ecosystems (Behling, 1995).

The second marked and synchronous climate change to even wetter conditions in the Llanos Orientales is evidenced by an expansion of forested area dated at 3860 $^{14}C$ yr BP at Laguna Angel and 3680 $^{14}C$ yr BP at Laguna Sardinas. This event is dated in the record of Laguna Loma Linda at 3590 $^{14}C$ yr BP. It is interesting to note that the pollen record of Laguna de Agua Sucia (Wijmstra and Van der Hammen, 1966), located about 35 km northwest of Loma Linda and representing the period of ca. 5500 to ca. 1000 $^{14}C$ yr BP, also indicates an increase in precipitation after ca. 3700 $^{14}C$ yr BP. A plausible explanation for both synchronous climatic changes from drier to wetter conditions may relate to a greater latitudinal range for the annual migration of the intertropical convergence zone (ITCZ).

The Loma Linda record also confirms that the lower terrace of the middle Caquetá river basin in the central Colombian Amazon was better drained during the early Holocene than during the last 3000 $^{14}C$ yr BP, primarily as a result of climate change (Behling *et al*., 1999).

Most of the pollen records from the Llanos Orientales (Behling and Hooghiemstra, 1998, 1999) and from the Gran Sabana (Rull, 1992), document a marked increase of *Mauritia* around 3500 $^{14}C$ yr BP. Even today this palm presents an important floral component in the landscape. In the Loma Linda record the expansion of *Mauritia* starts around 2300 $^{14}C$ yr BP. The general expansion of *Mauritia* palms, as documented from many sites in the Llanos Orientales, may relate on the one hand to the inferred increase in precipitation (Kahn, 1987; Kahn and De Granville, 1992), and on the other to stronger human impact (Behling and Hooghiemstra, 1998, 1999). Human impact on the savanna ecosystem seems to be very strong, especially during the late Holocene. We consider that the vegetation of the mid-Holocene period was little influenced by humans and conclude that the dynamics of the forest–savanna boundary are determined primarily by precipitation change, and to a lesser extent to changes in fire frequency, soil conditions and biotic factors (Furley, 1992; Furley *et al*., 1992; Ross *et al*., 1992).

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