



Late Holocene rainforest disturbance in French Guiana

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Abstract

Palm swamp forest sediments collected in French Guiana provide new data about late Holocene rainforest. Two cores were collected in 'Les Nouragues' ecological station (4°05'N, 52°40'W). The lithology shows two different types of sediment, organic peat in the upper part and oxidized clay with low organic content and lacking pollen in the lower part, both separated by a gravel horizon. Radiocarbon dates show that this gravel horizon could have been deposited between 4500 and 3000 yr BP. Pollen analysis carried out on the organic sediments record rainforest disturbances between ca 1520–1380 and 1060–860 cal yr BP suggested by the presence of the pioneer tree species *Cecropia* together with other shade intolerant genera. *Cecropia* is recorded for a period that lasts between 660 and 320 years. This abnormal duration for presence of a pioneer species in rainforest is explained by brief and repeated changes in the composition of the canopy associated to perturbations of the palm swamp. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

The history of tropical lowland rainforests, especially during the last several thousand years, is influenced by both climate variability and human impact. Presence of cultivated plant remains (Bush and Colinvaux, 1994), increase of charcoals particles concentration (Kershaw et al., 1997), stone tools (Meggers, 1994), ceramics (Lathrap, 1970), changes in vegetation composition due to slash, burning and agriculture (Semah et al., 1992) are used to evaluate human occupation and impact on rainforest dynamics. On the other hand, climate also had a strong impact on rainforest habitats during the Holocene: flooding, aridity, hurricanes have been recorded and attested through strong changes in vegetation composition and/or increase of charcoals

particles (Liu and Colinvaux, 1988; Kershaw, 1995; Vincens et al., 1998; Haberle and Ledru, 2001). Separating both influences has in general been quite difficult.

To document rainforest dynamics during the Late Holocene, we analyzed for the first time two records in French Guiana, a poorly inhabited area and one of the tropical regions with exceptionally high precipitation. Large areas remain covered by mature lowland rainforest, and recently the region was recognized to be of great importance for biodiversity conservation and became an ecological park. Archaeological studies in the Guianan hyper-humid forest region, especially in the Petit Saut area, have not uncovered any remains of human occupation prior to 2100 yr BP.

2. Present environmental setting

Research was conducted at the Nouragues field

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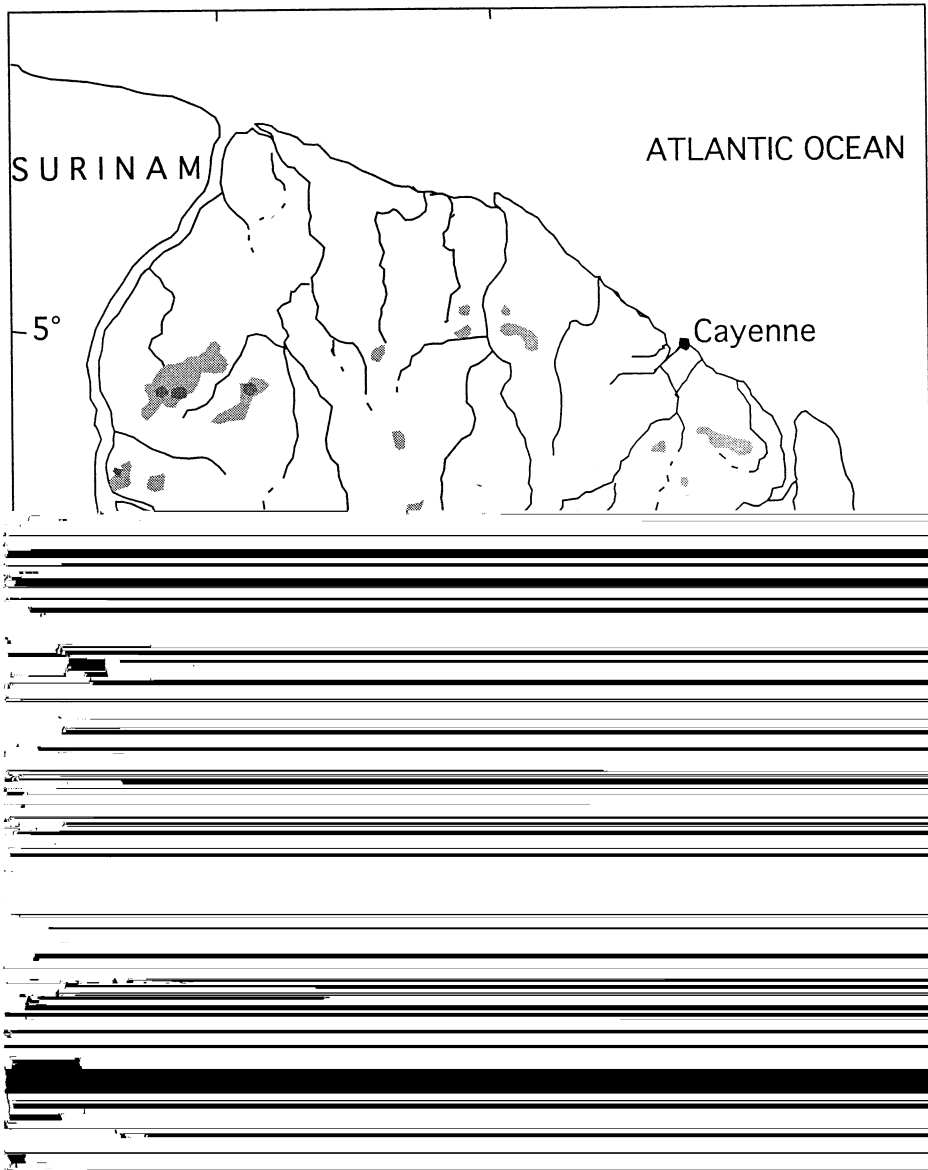


Fig. 1. Location of Les Nouragues in French Guiana.

station located about 100 km inland ($4^{\circ}05'N$, $52^{\circ}40'W$) in a hilly region where several granitic outcrops ('inselbergs') occur between 300 and 450 m high (Fig. 1). No longterm data on rainfall are available but between 1990 and 1994, the average annual rainfall was about 2920 mm. The Inter Tropical Convergence Zone (ITCZ) or Meteorological Equator (ME) is the essential precipitation supplier

of the tropical zone. The ME shifts latitudinally on both sides of the Equator creating a bimodal precipitation regime with two precipitation maxima. Precipitation patterns over the region can be affected by the El Nino/Southern Oscillation in response to southward shift of this convection zone that is normally centered on Amazonia (Diaz and Markgraf, 1992). As a consequence, precipitation decreases in northern

South America, northeastern Brazil and Amazonia. In French Guiana, a distinct dry season is recorded from September to November and a less conspicuous drier period in February and March, and mean annual temperature is about 26.1°C. Vegetation at the Nouragues station is mainly composed of rainforest except for the tops of the ‘inselbergs’ where, at 434 m elevation, dry forest and savannas are found. The forest is old-growth evergreen rainforest, with a canopy height ranging between 20 and 40 m, with some individual trees emerging above the canopy up to 60 m. Botanical surveys have been carried out since 1987 and collected plants (about 1300 species) are compiled in a database (Hoff et al., 1989; Sabatier and Prevost, 1992). The five most common tree taxa are in the families of Lecythidaceae, Caesalpiniaceae, Sapotaceae, Chrysobalanaceae and Burseraceae.

The sediment cores were collected in a peaty swamp (also called pinotière in French) areas characterized by the palm tree *Euterpe oleracea*, and plants in the families Cyclanthaceae, Araceae, Bromeliaceae and Orchidaceae. On the dry fringes of the swamp occur *Virola surinamensis* (Rol.) Warb. (Myristicaceae), *Symphonia globulifera* L. (Clusiaceae), *Pterocarpus officinalis* Jacq. (Fabaceae), *Carapa guianensis* Aubl. (Meliaceae) and *Eschweilera* sp. (Lecythidaceae) (Oldeman, 1969). In Les Nouragues pollen spectra *Virola* and *Symphonia* are indicators of the palm swamp as other taxa are either poorly preserved or are poor pollen producers. These swamps are seasonally flooded and largely composed of organic sediments. Most tropical forests have high taxa diversity, and a considerable proportion of the species tend to have a widely scattered distribution. Because of these characteristics, the number of pollen types in the sediments recovered is very high, but many types occur in low numbers.

3. Material and methods

Two cores of 370 (NO 92-2) and 500 cm (NO 92-3) length were drilled at the Nouragues swamp site ca 100 m apart with vibra coring equipment (Martin and Flexor, 1989). Core samples were processed for seed (Charles-Dominique et al., 1998) and pollen content. Samples for pollen analysis were treated following the standard palynological techniques, applying the Lubert

technique (50% HNO₃ solution and 10% KOH solution). Palynomorphs were separated using a ZnCl₂ solution of density 2 and mounted in glycerine for light microscopical analysis. Pollen and spores were identified with 1000× magnification by comparison with our pollen reference collection (500 taxa collected at the ORSTOM Herbarium at Cayenne and 600 taxa characteristic of Brazilian tropical forests) and the pollen atlas by Roubik and Moreno (1991). At least 400 pollen grains were counted at each level. Pollen taxa are grouped into arboreal, climbers, non-arboreal, aquatic and unknown categories and are expressed as a percent of the pollen sum. Aquatics, wetland taxa and spores were excluded from the pollen sum and expressed as a percent of the pollen sum (Faegri and Iversen, 1989). All identified taxa are listed in Appendix A and the detailed pollen counts are available in the NOAA-World Data Center A for Paleoclimatology (Latin American Pollen Database). 158 arboreal taxa, 48 climber and epiphyte taxa, 31 non-arboreal taxa, 5 aquatic and 7 fern taxa were identified and between 5 and 10% remained unidentified.

4. Stratigraphy and chronology

Both cores, NO 92-2 and NO 92-3, collected at the Nouragues site show similarities in their lithology (Figs. 2 and 3). The upper portion of the core is composed of organic peat separated by a level of gravel between ca 130 and 140 cm depth, respectively, from the lower, oxidized part with low organic content and lacking pollen. Radiocarbon dates (Table 1) show that this gravel level could have been deposited between 4500 and 3000 yrs BP. Radiocarbon dates for NO 92-2 at 141 cm depth gave 3040 ± 70 yrs BP and at 67–71 cm depth 1570 ± 50 yrs BP. Radiocarbon dates for NO 92-3 gave 4330 ± 60 yrs BP at 114–119 cm depth for the organic clay above the gravel layer and 2530 ± 40 yrs BP immediately above at 109–112 cm depth. This latter date is rejected because a similar date was obtained on a piece of root located in the oxidized clay above the gravel. Another date of 2930 ± 110 was obtained on less than 1 g micro-charcoal fragments at 90–93 cm depth and is doubtful; other dates of 1890 ± 40 yrs BP on total organic matter at 62–67 cm depth, of

1300 ± 40 yrs BP at 36–37 cm depth on vegetal fibers and 1300 ± 60 yrs BP at 32–38 cm depth on wood. Modern levels are reached at 10–14 cm depth with an age of 50 ± 50 yrs BP on organic matter. Sedimentation rates are 0.045 cm/yr for NO 92-2 and 0.08 cm/yr for NO 92-3.

5. Palynological records

Results of core NO 92-2 have already been described by Ledru et al. (1997) and a brief summary will be given here using calibrated ¹⁴C dates (Stuiver and Becker, 1993). Results of core NO 92-3 will be compared with NO 92-2 with summary pollen diagrams (Figs. 2–4).

5.1. NO 92-2 record

In core NO 92-2, the pollen content of 50 samples was analyzed covering the upper 131 cm. Twenty-six significant taxa are illustrated in the simplified diagram in Fig. 2. Four local pollen zones (D to A) can be recognized. The pollen spectrum on the top of the diagram is a surface sample and represents the modern pollen deposition. Zone D extends from 131 to 85 cm, calibrated between 3124–2785 and 2124–1679 cal yr BP is characterized by high tree pollen frequencies (70–85%), mainly *Symphonia* (10–37%), climbers of the *Sabicea* type (1–5%) (Rubiaceae) and *Marcgravia* (10–22%) (Marcgraviaceae) and local swamp vegetation (Alismataceae and *Cyathea* (15%)). The water level probably was stable (presence of Alismataceae) which suggests the absence of a dry season during this period. A single pollen grain of *Podocarpus* was determined in sample 37 at 96.5–99 cm depth. This zone is the most diverse of the whole core. Zone C extends from 85 to 71 cm, calibrated between 2124–1679 and 1525–1375 cal yr BP, and reflects a change in the forest cover as shown by an increase of *Ficus* (5–20%) (Moraceae), *Schefflera* (1–6%) (Araliaceae), *Virola* (9–21%), Mimosaceae (1–6%) and *Cecropia* (up to 5%) (Cecropiaceae) and a decrease of climbers, ferns and *Symphonia*. *Cecropia* is a pioneer tree of the rain-forest which grows in open sites. Zone B, extends from 71 to 50 cm (samples 25 to 17), and is calibrated to date between 1525–1375 and 1058–863 cal yr BP. This zone is characterized by the dominance of

Cecropia (52%), *Ficus* (5–15%) and *Vismia* type (2–43%) (Clusiaceae). The other tree taxa, *Tetragastris*-type (Burseraceae) (0.5%), *Symphonia* (5–0.5%), *Virola* (18–2%) and *Tapirira* (Anacardiaceae) (1.5–0.1%) decrease and Melastomataceae increase (4–18%). The swamp forest must have disappeared at that time. This zone reflects the maximum opening of the vegetation, which started in the previous zone, as shown by the presence of *Cecropia*, *Vismia* and Melastomataceae. In Guiana, most representatives of the Melastomataceae are shade intolerant and indicators of open forests. Open forest conditions lasted between 660 years at a maximum and 320 years at a minimum, between 1520 and 860 cal yr BP. There is a clear gradual opening up of the forest from zone D–B with a shift in arboreal dominance from *Hyeronima*, *Schefflera*, *Ficus*, *Cecropia*, which may suggest a progressive increase in disturbance frequency beginning as early as just after 3150 cal yr BP. In zone A, which extends from 50 to 0 cm, between 1058/863 and 0 cal yr BP, the forest cover and the palm swamp area increased, although the species composition of the surrounding forest is not the same as in zone D. The main taxa are in the families of Fabaceae and Caesalpiniaceae, represented by *Andira*-type and *Pterocarpus*, and *Doliocarpus*-type (Dilleniaceae). *Schefflera*, *Symphonia*, *Virola*, Melastomataceae are also present, climbers are dominated by *Heteropteris*-type (12%) (Malpighiaceae), and non-arboreal pollen with Asteraceae. The species diversity did not reach the high frequency found in zone D. A short opening in tree cover is detected between 660 and 420 cal yr BP (sample 8) with an increase of *Cecropia* (3%) and *Ficus* (30%). Disappearance of ferns, increase of Asteraceae, Fabaceae and Caesalpiniaceae document a different forest composition compared to zone D.

5.2. NO 92-3 record

Forty three samples have been analysed in core NO 92-3, covering the upper 133 cm. Below 133 cm, no pollen was preserved. Frequency of arboreal pollen is high throughout the record, ranging from 70 to 55%. Twenty-eight most frequent taxa were selected and plotted (Fig. 3). Based on changes in pollen proportions we recognized five pollen zones in the simplified

Les Nouragues 92 - 2

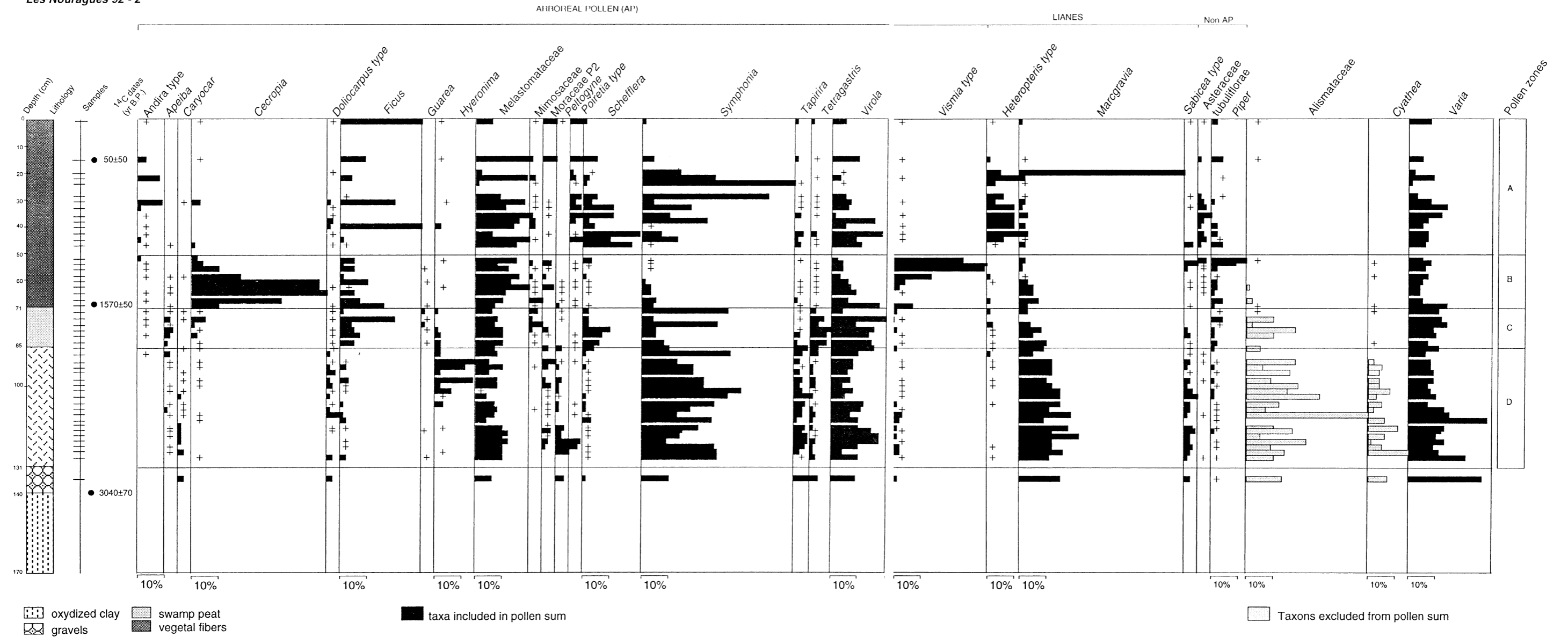


Fig. 2. Core NO 92-2. Summary pollen percentage diagram based on pollen sum (excluding aquatics and wetlands taxa).

Les Nouragues 92-3

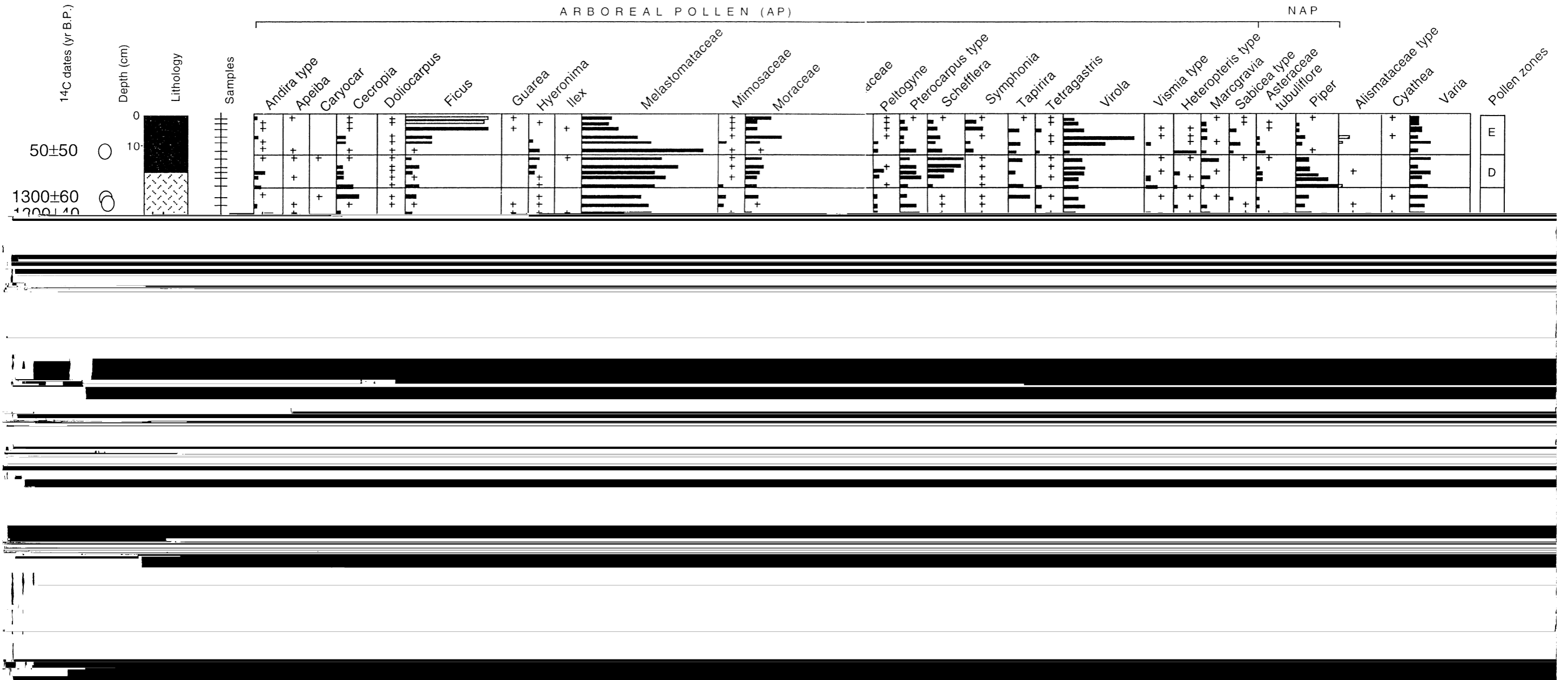


Fig. 3. Core NO 92-3. Summary pollen percentage diagram based on pollen sum (excluding aquatics and wetland taxa).

diagram numbered from A, the youngest to E the oldest. Zone E, extends from 133 to 69 cm, with an estimated age of 2750–2360 to 1892–1714 cal yr BP and is characterized by high frequencies of Melastomataceae (ranging from 24 to 8%), *Viola* (ranging from 1 to 8%), *Pterocarpus* (0.3–8.5%), Moraceae (0–23%), *Schefflera* (0.1–4%), *Symphonia* (1–10%) *Tetragastris* (0–7%) and the climber *Marcgravia* (0.2–10%). Frequencies of *Marcgravia*, Moraceae and *Cecropia* start to increase at the end of zone E. Also represented in zone E are *Andira* type, *Apeiba*, *Caryocar*, *Doliocarpus*, *Ficus*, *Hyeronima*, Mimosaceae, Myrtaceae, *Peltogyne*, *Sabicea* type, Asteraceae tubuliflorae and *Piper*. Zone D, which extends from 69 to 53 cm, estimated age ca 1892–1714 cal yr BP, is characterized by the disappearance of *Symphonia*, decrease in *Marcgravia* (ranging between 2 and 5%), *Cecropia* (frequencies 2–4%), and Moraceae (4–8%), and increased presence of *Ilex*. *Andira* type, *Ficus*, *Hyeronima*, Melastomataceae, *Piper*, *Pterocarpus*, *Schefflera* and *Viola* represent the remaining major taxa. A single pollen grain of *Podocarpus* has been determined in sample 27, at 60–62.5 cm depth. Zone C extends from 53 to 26 cm, with an estimated age between 1892–1714 and 1305–1066 cal yr BP, and is characterized by the disappearance of *Symphonia* and *Schefflera*, the decrease of *Viola* (2–5%) and the increase of Melastomataceae (12–6%), *Piper* (3–13%), *Tapirira* (0–8%) and Asteraceae tubuliflorae (0–1.5%). *Andira*-type, *Cecropia*, *Ficus*, *Hyeronima*, Mimosaceae, Moraceae, *Pterocarpus*, *Heteropteris*, *Marcgravia* are also present. The decrease in *Viola* and *Symphonia* pollen frequencies could be attributed to a reduction of the palm swamp forest due to a decrease in moisture. Zone B extends from 26 to 12 cm, estimated age of 1300–1070 to 100 cal yr BP, and is characterized by the dominance of Melastomataceae (26–45%), continuing absence of *Symphonia* pollen and of *Cecropia* (0.5–3%), *Tapirira* (0–4%) and *Piper* (9–0.5%). Pollen of *Andira*-type, *Ficus*, *Hyeronima*, Moraceae, *Pterocarpus*, *Viola* and Asteraceae tubuliflorae are present. Zone A extends from 12 to 0 cm and represents the present-day vegetation as shown by the high frequencies of *Ficus* pollen grains. A huge *Ficus* tree is growing right in the middle of the palm swamp. This zone is also characterized by an increase of *Symphonia* and

Viola and a decrease in Melastomataceae (24–7%), *Pterocarpus* (0.1–1.7%), *Schefflera* (4–0.8%), Asteraceae tubuliflorae (1.5–0%), and *Piper* (3–0.5%). The palm swamp seems to have recovered compared to the previous zone.

5.3. Comparison of the records

A comparison of the records show a coeval development of taxa. In the NO 92-2 record *Cecropia* peaks between 71 and 50 cm depth; in NO 92-3, instead of showing a peak, the pioneer species seems to be present throughout the record, with higher frequencies between 93 and 35 cm. At the same time, the frequencies of the palm swamp species *Viola* and *Symphonia* decrease suggesting palm swamp perturbations. *Piper* peaks right after the *Cecropia* and is immediately followed by an increase of Melastomataceae/Combretaceae, *Schefflera*, *Pterocarpus*-type and *Viola* frequencies, suggesting that the palm swamp reconstitution. The depths where these coevents are observed do not correspond between both records. Radiocarbon dates from NO 92-3 indicate a faster sedimentation rate for NO 92-3 than for NO 92-2. Therefore we suggest that the interval between 93 and 35 cm depth in NO 92-3 corresponds to pollen zone B in NO 92-2. Summary diagrams (Fig. 4) are used to correlate both records. These diagrams group arboreal pollen (excluding *Cecropia*), the pioneer taxa *Cecropia*, climbers and non-arboreal pollen. Percentages of each group are calculated with respect to the pollen sum.

These results suggest that the open forest recorded in NO 92-2 did not extend to the present but existed only locally during several centuries.

6. Discussion

Pioneer species colonizing a canopy gap are rapidly taken over by mature forest species in a few decades. The persistence of pioneer plant species such as *Cecropia* for several centuries would suggest brief and repeated disturbances occurring every 10 to 30 years. Canopy gaps, observed today, are created by the fall of trees either by snapping or uprooting, falling branches, or the death of a tree. Windstorms are a common cause for tree falls. The number and size of gaps formed each year varies substantially and may be

related to variability in annual rainfall. In Nouragues, annual gap area varies between 0.64 and 1.33% and the density of pioneer species increases with increasing gap size. The rate of gap closure ranges between 5 and 10 years related to the size of the gap (Riéra, 1985; Riéra and Alexandre, 1988; van der Meer and Bongers, 1996a,b). Studies show that tree falls peak during the rainy season: large trees fall more frequently at the start of the rainy season than during the dry season. Trees often fall during calm weather, suggesting that the fall is caused by the heavy load of the tree crown. Exogenous factors such as wind and rain, which cause tree falls are most likely to affect the larger trees in the forest. In India, many forest trees fall most often at the start and the middle of the rainy season (Chandrasekara and Ramakrishnan, 1994) and in Mexico, Martinez-Ramos et al. (1988) found a positive correlation between variability in rainfall and gap formation. More frequent uprooting is also observed near creeks and is related to unstable soils (Durrieu de Madron, 1994). On Barro Colorado Island (Panama), Hubbell and Foster (1990) attributed the high tree mortality of 3% p.a. (usually between 1 and 2%) to the prolonged and severe 1983 dry season associated with the El Niño drought. But the high mortality rates of trees in the large size classes at Barro Colorado Island have not been documented for other tropical sites. The more typical consequence of drought is high mortality among the small size-classes. In

tropical wet forests, Hartshorn (1990) observed high mortality of seedlings and saplings during long (4–8 weeks) rainless periods. At wet sites larger trees appear to be unaffected by short droughts, possibly because of their more sensitive root systems. Therefore we suggest that the persistence of the pioneer species *Cecropia* could be related to repeated and short events that contributed in maintaining the canopy gap at Les Nouragues during at least 320 years and at maximum 660 years, between 1525 and 865 cal yr BP.

An erosional event was detected in Ecuadorian rainforest at ca 4000 yr BP and changes in vegetation cover are recognized between 1300 and 800 yr BP (Liu and Colinvaux, 1988; Bush and Colinvaux, 1988). In Amazonia, at Carajas, a lake located in the dry Amazonian corridor, the pollen and mineralogical records attest a dry episode before 4000 yr BP and several short dry events afterwards (Sifeddine et al., 1994; Turcq et al., 1998). The paleodata indicate that these events were concomitant with short dry climate episodes whose frequency varied during the last 7000 years (Martin et al., 1993). Studies on soil organic matter dynamics using carbon isotopes as indicators in a savanna-forest boundary area (Humaíta, southern Amazonia) show that savanna vegetation expanded at least 2 km into the modern forest ecotone during the mid Holocene, and a forest expansion appears during the last 1000 years (Pessenda et al., 1998). Geomorphological studies give insights into the past

Table 1

Radiocarbon dates from material collected in French Guiana. Calibrated radiocarbon dates follow Stuiver and Becker (1993) and are quoted as minimum and maximum age range at two standard deviations

| Lab. number and depth (cm) | Material | ¹⁴ C dates (yr BP) | Cal. ages (yr BP) |
|----------------------------|-----------------|-------------------------------|-------------------|
| <i>NO 92-3</i> | | | |
| OBDY 1172 (10–14) | Organic matter | 50 ± 50 | |
| Beta 94239 (32–38) | Wood | 1300 ± 60 | 1300–1070 |
| Beta 110213 (36–37) | Vegetal fibers | 1300 ± 40 | 1290–1140 |
| OBDY 1288 (62–67) | Organic matter | 1890 ± 40 | 1890–1710 |
| Beta 94330 (90–93) | Micro charcoals | 2930 ± 110 | 3360–2780 |
| Beta 66544 (235) | Wood | 2520 ± 50 | 2750–2360 |
| Beta 110214 (109–112) | Wood | 2530 ± 40 | 2750–2470 |
| OBDY 1148 (114–119) | Organic matter | 4330 ± 60 | 5040–4730 |
| <i>NO 92-2</i> | | | |
| OBDY 1172 (10–14) | Wood | 50 ± 50 | |
| OBDY 1151 (67–71) | Wood | 1570 ± 50 | 1520–1380 |
| Beta 66543 (141) | Vegetal fibers | 3040 ± 70 | 3340–3060 |

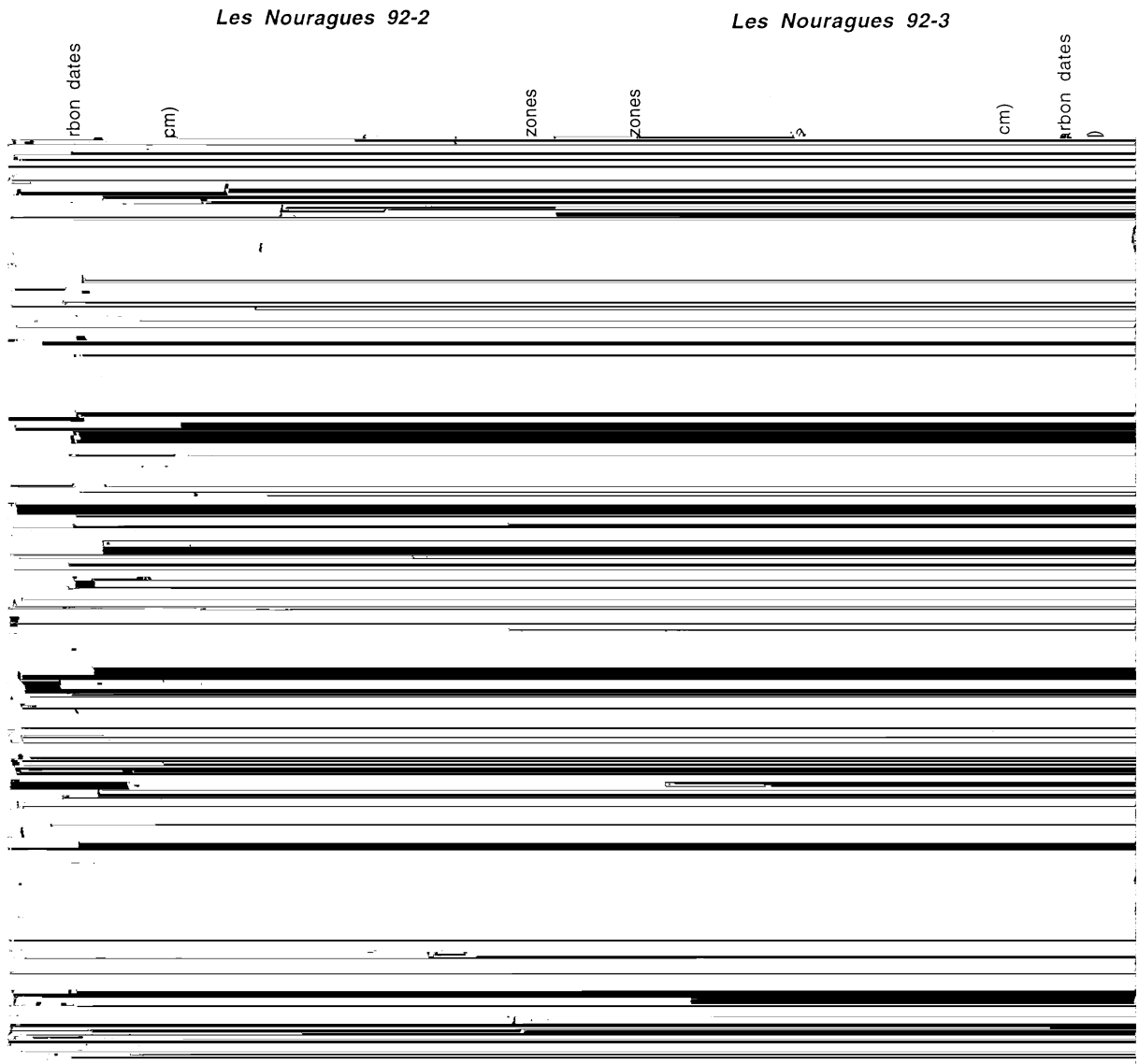


Fig. 4. Main pollen percentage diagrams of cores NO 92-2 and NO 92-3 showing radiocarbon dates and downcore changes in the representation of four main ecological groups. The supposed correlation between both records is indicated.

movements of creek meanders during the different moist climate phases. In the humid forest zones of the Peruvian Andes foothills (Dumont and Fournier, 1994) showed that during the last 3000 years, the river outflows clearly decreased during the 2000–1300 and 900–500 yrs BP periods. Meggers (1994) evaluated the existence and intensity of short term climatic fluctuations in Amazonia during the past 2000 years from

archeological sequences. She used charcoal concentration the soils to determine periods of dryness. On this basis she detected dry events at 1500, 1000, 700 and 400 yrs BP. Although these changes could be associated with early agriculture activity, we must keep in mind that increased climatic variability may enhance the environmental impact of anthropogenic activity.

7. Conclusion

Our results suggest that during the last 4500 yrs BP openings of the rainforest tree cover occurred at least two times in 'Les Nouragues'. The first one is indicated by a thick gravel level in which pollen was not preserved between ca 4500 and 3000 yrs BP. The second period is shown by the prolonged presence of the pioneer species *Cecropia* between 1520 and 860 cal yrs BP. This episode is characterized by repeated, short events that contributed to maintaining the canopy gap at Les Nouragues. We are not able to conclude whether these perturbations of the rainforest canopy are due to human impact or are natural, although such openings were also recorded in other rainforest ecosystems. More pollen or charcoal analysis of late Holocene sequences are needed to improve our knowledge of man/climate impacts history in rainforest areas.

Acknowledgements

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Appendix A. List of the taxa determined in both Les Nouragues records; H means Heliophilous taxa, climbers being considered as heliophilous in general

AP (Arboreal Pollen)

| | | |
|---------------------------------------|---|----------------------------------|
| Aegiphila (Verbenaceae) H | Clerodendrum type (Verbenaceae) | Hippocrateaceae sp. |
| Alchornea (Euphorbiaceae) | Cochlospermum (Cochlospermaceae) | Hirtella (Chrysobalanaceae) |
| Alnus (Betulaceae) | Copaifera type (Caesalpiniaceae) | Humiria (Humiriaceae) |
| Amaouia (Rubiaceae) | Cordia (Boraginaceae) | Hyeronima (Euphorbiaceae) H |
| Andira t. (Fabaceae) | Couma type (Apocynaceae) | Hymenea (Caesalpiniaceae) |
| Apeiba (Tiliaceae) H | Couratari (Lecythidaceae) | Ilex (Aquifoliaceae) |
| Apuleia (Caesalpiniaceae) | Coutarea type (Rubiaceae) | Iryanthera (Myristicaceae) |
| Ardisia (Myrsinaceae) | Cupania (Sapindaceae) | Ixora type (Rubiaceae) |
| Arecaceae C1 | Cybianthus (Myrsinaceae) | Jacaranda (Bignoniaceae) H |
| Aspidosperma (Apocynaceae) | Dalbergia type (Fabaceae) | Lacistema t. (Flacourtiaceae) |
| Astrocaryum (Arecaceae) | Dendrobengia (Icacinaceae) | Lacmellea (Apocynaceae) |
| Astronium (Anacardiaceae) | Desmodium type (Fabaceae) | Laetia (Flacourtiaceae) H |
| Banara guianensis. (Flacourtiaceae) H | Dialium type (Caesalpiniaceae) | Lafoensia (Lythraceae) |
| Bertiera (Rubiaceae) | Dicorynia type (Caesalpiniaceae) | Lecythidaceae |
| Bocoa type (Fabaceae) | Diospyros (Ebenaceae) | Licania (Chrysobalanaceae) |
| Bombacopsis type (Bombacaceae) | Diospyros cf. <i>duckei</i> (Ebenaceae) | Lithraea type (Anacardiaceae) |
| Bunchosia type (Malpighiaceae) | Eperua falcate (Caesalpiniaceae) | Luehea (Tiliaceae) |
| Caesalpinia (Caesalpiniaceae) | Eperua rubiginosa (Caesalpiniaceae) | Lythraceae |
| Carapa type (Meliaceae) | Erythroxylum (Erythroxylaceae) | Mabea (Euphorbiaceae) |
| Carpotroche (Flacourtiaceae) | Eschweilera (Lecythidaceae) | Maprounea type (Euphorbiaceae) H |
| Caryocar (Caryocaraceae) | Faramea (Rubiaceae) | Margaritaria (Euphorbiaceae) |
| Casearia type (Flacourtiaceae) | Ficus (Moraceae) | Matayba (Sapindaceae) |
| Cassia (Caesalpiniaceae) | Gallesia type (Rubiaceae) | Mayna (Flacourtiaceae) |
| Cecropia (Cecropiaceae) H | Goupia (Celastraceae) H | Maytenus type (Celastraceae) |
| Cedrela type (Meliaceae) | Guapira type (Nyctaginaceae) | Melastomataceae |
| Cestrum type (Solanaceae) | Guarea (Rubiaceae) | Meliaceae sp |
| Chimarrhis (Rubiaceae) | Guazuma type (Sterculiaceae) H | Meliaceae/Sapotaceae |
| Chrysophyllum (Sapotaceae) | Guettarda (Rubiaceae) | Miconia type (Melastomataceae) |
| | Hasseltia (Flacourtiaceae) H | Micropholis type (Sapotaceae) |

Mimosaceae
Miquartia (Olacaceae)
Moraceae P2
Myrtaceae
Neea type (Nyctaginaceae) H
Noisettia (Violaceae)
Oxandra (Annonaceae)
Palicourea (Rubiaceae) H
Paloue (Fabaceae)
Pausandra (Euphorbiaceae)
Peltogyne (Caesalpiniaceae)
Pisonia (Nyctaginaceae)
Podocarpus (Podocarpaceae)
Pterocarpus (Fabaceae)
Poraqueiba (Icacinaceae)
Posoqueria (Rubiaceae)
Pouteria (Sapotaceae)
Pouteria caimito (Sapotaceae)
Pradosia type (Sapotaceae)
Protium sagotianum (Burseraceae)
Pseudobombax (Bombacaceae)
Psychotria (Rubiaceae)
Pterodon type (Fabaceae)
Pterogyne type (Caesalpiniaceae)
Qualea (Vochysiaceae)
Quararibea (Bombacaceae)
Quiina (Quiinaceae)
Rinorea (Violaceae)
Roupala (Proteaceae)
Rutaceae sp
Ryania (Flacourtiaceae)
Sacoglottis (Humiriaceae)
Sapium (Euphorbiaceae) H
Sapotaceae sp
Schefflera type =
Didymopanax type (Araliaceae) H

References

- Bush, M., Colinvaux, P., 1988. A 7000-year pollen record from the amazon lowlands, Ecuador. *Vegetatio* 76, 141–154.
- Bush, M.B., Colinvaux, P.A., 1994. A paleoecological perspective of tropical forest disturbance: records from Darien, Panama. *Ecology* 75 (6), 1761–1768.
- Chandrashekhara, U.M., Ramakrishnan, P.S., 1994. Vegetation and gap dynamics of a tropical wet evergreen forest in the western Ghats of Kerala, India. *J. Tropical Ecol.* 10, 337–354.
- Charles-Dominique, P., Blanc, P., Larpin, D., Ledru, M.P., Riera, B., Sarthou, C., Servant, M., Tardy, C., 1998. Forest perturbations and biodiversity during the last ten thousand years in French Guiana. *Acta Oecol.* 19, 295–302.
- Diaz, H.F., Markgraf, V., 1992. *El Niño*. Historical and Paleoclimatic Aspects of the Southern Oscillation. Cambridge University Press.
- Dumont, J.F., Fournier, M., 1994. Geodynamic environment of Quaternary morphostructures of the subandean foreland basins of Peru and Bolivia: characteristics and study methods. *Quat. Int.* 21, 129–142.
- Durrieu de Madron, 1994. Mortalité des arbres en forêt primaire de Guyane française. *Bois forêts Tropiques* 239, 43–57.
- Fægri, K., Iversen, J., 1989. *Textbook of Pollen Analysis*. Fourth ed. Wiley, Chichester.
- Haberle, S.G., Ledru, M.-P., 2001. Correlations among charcoal records of fires from the past 16,000 years in Indonesia, Papua-New Guinea and Central and South America. *Quaternary Research* 55, 97–104.
- Hartshorn, G.S., 1990. An overview of neotropical forest dynamics. In: Gentry, Al. H. (Ed.), *Four Neotropical Rainforests*. Yale University Press, London, pp. 585–599.
- Hoff, M., Cremers, G., Feuillet, C., de Granville, J.J., 1989. La banque de données 'Aublet' de l'Herbier du centre ORSTOM de Cayenne (CAY). *Bull. Jardin Bot. Nat. Belg.* 59, 171–178.
- Hubbell, S.P., Foster, R.B., 1990. Structure, dynamics, and equilibrium status of old-growth forest on Barro Colorado Island. In: Gentry, Al. H. (Ed.), *Four Neotropical Rainforests*. Yale University Press, London, pp. 522–541.
- Kershaw, P., 1995. Environmental change in Greater Australia. Transitions Pleistocene to Holocene in Australia and Papua New Guinea, Allen, J., O'Connell, J. (Eds.). *Antiquity* 69 (265), 656–675.
- Kershaw, A.P., Bush, M.B., Hope, G.S., Weiss, K.F., Goldammer, J.G., Sanford, R., 1997. The contribution of humans to past biomass burning in the tropics. In: Clark, J.S., Cachier, H., Goldammer, J.G., Stocks, B. (Eds.), *Sediment Records of Biomass Burning and Global Change*. Springer, New York, pp. 413–442.
- Lathrap, D.W., 1970. The upper Amazon. In: Glyn, D. (Ed.), *Ancient People and Places*, vol. 70. Thames and Hudson, London.
- Ledru, M.P., Blanc, P., Charles-Dominique, P., Fournier, M., Martin, L., Riéra, B., Tardy, C., 1997. Reconstitution palynologique de la forêt guyanaise au cours des 3000 dernières années. *C. R. Acad. Sci. Paris t.324 IIA*, 469–476.
- Liu, K.B., Colinvaux, P., 1988. A 5200-year history of Amazon rainforest. *J. Biogeogr.* 15, 231–248.
- Martin, L., Flexor, J.M., 1989. Vibro-testemunhador leve: construção, utilização e possibilidades. *Proc. 2do Congresso da ABEQUA*, Rio de Janeiro, p.14.
- Martin, L., Fournier, M., Mourguiart, P., Sifeddine, A., Turcq, B., Absy, M.L., Flexor, J.M., 1993. Southern oscillation signal in South American paleoclimate data of the last 7000 years. *Quat. Res.* 39, 338–346.
- Martinez-Ramos, M., Alvarez-Buylla, E., Sarukhan, J., Pinero, D., 1988. Treefall age determination and gaps dynamics in a tropical rainforest. *J. Ecol.* 76, 700–716.
- Megggers, B., 1994. Archeological evidence for the impact of mega-Niño events on Amazonia during the past two millenia. *Clim. Change* 28, 321–338.
- Oldeman, R.A.A., 1969. Etude biologique des pinotières de la Guyane française. *Cahiers ORSTOM Ser. Biol.* 10, 3–18.
- Pessenda, L.C.R., Gomes, B.M., Aravena, R., Ribeiro, A.S., Boulet, R., Gouveia, S.E.M., 1998. The carbon isotope record in soils along a forest-cerrado ecosystem transect: implications for vegetation changes in the Rondonia state, southwestern Brazilian Amazon region. *The Holocene* 8, 631–635.
- Riéra, B., 1985. Importance des buttes de déracinement dans la régénération forestière en Guyane Française. *Rev. Ecol. (Terre & Vie)* 40, 321–329.
- Riéra, B., Alexandre, D.Y., 1988. Surface des chablis et temps de renouvellement en forêt dense tropicale. *Acta Oecol.* 9, 211–220.
- Roubik, D.W., Moreno, J.E., 1991. Pollen and spores of Barro Colorado Island. Missouri Botanical Garden.
- Sabatier, D., Prevost, M.F., 1992. Variations du peuplement forestier à l'échelle stationnelle: le cas de la station des Nouragues en Guyane française, In *Atelier MAB*, pp. 169–187.
- Semah, A.M., Semah, F., Guillot, C., Djubiantono, T., Fournier, M., 1992. Etude de la sédimentation pollinique durant les quatre derniers millénaires dans le bassin d'Ambarawa (Java Central, Indonésie). Mise en évidence de premiers défrichements. *C. R. Acad. Sci. Paris* 315 II, 903–908.
- Sifeddine, A., Frohlich, F., Fournier, M., Martin, L., Servant, M., Soubies, F., Suguio, K., Turcq, B., Volkmer-Ribeiro, C., 1994. La sédimentation lacustre indicateur de changements de paléoenvironnements au cours des 30 000 dernières années (Carajas, Amazonie, Brésil). *C. R. Acad. Sci. Paris* 312 II, 673–678.
- Stuiver, M., Becker, B., 1993. High precision decadal calibration of the radiocarbon time scale, AD 1950–6000 BC. *Radiocarbon* 35, 5–65.
- Turcq, B., Sifeddine, A., Martin, L., Absy, M.L., Soubies, F., Suguio, K., Volkmer-Ribeiro, C., 1998. Amazonia rainforest fires: a lacustrine record of 7000 years. *Ambio* 27 (2), 139–142.
- Van der Meer, P.J., Bongers, F., 1996a. Formation and closure of canopy gaps in the rainforest at Nouragues, French Guiana. *Vegetatio* 126, 167–179.
- Van der Meer, P.J., Bongers, F., 1996b. Patterns of treefalls and branchfalls in a tropical rainforest in French Guiana. *J. Ecol.* 84, 19–29.
- Vincens, A., Schwartz, D., Bertaux, J., Elenga, H., de Namur, C., 1998. Late Holocene climatic changes in Western equatorial Africa inferred from pollen from Lake Sinnda, Southern Congo. *Quat. Res.* 50, 34–45.