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LATE PLIOCENE–PLEISTOCENE HIGH RESOLUTION POLLEN SEQUENCE OF COLOMBIA: AN OVERVIEW OF CLIMATIC CHANGE

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Two long continental pollen records, Funza I (357 m) and Funza II (586 m) from the high plain of Bogotá (Colombia) at 2550 m elevation, have been studied palynologically. Fission track dates on zircon from intercalated volcanic ashes provided a chronological framework and showed the pollen records, which correlate with high precision, to be continuous over the interval from ca. 3.2 Ma to ca. 27 ka. The Late Pliocene–Pleistocene history of the montane forests and open alpine paramo vegetation is documented with a temporal resolution of ca. 6–5 ka, and for the upper 1.1 Ma with a resolution of ca. 1.2 ka. The immigration of the northern hemisphere elements *Alnus* (at ca. 1 Ma) and *Quercus* (at ca. 0.33 Ma), which travelled along the Panamanian landbridge, caused significant changes in the composition of the Andean montane forests. The successive Pleistocene glaciations forced the Andean vegetation belts to an almost continuous altitudinal movement; the upper forest line (at present at ca. 3200 m) shifted between 1800 m (glacials) and ca. 3500 m (interglacials), corresponding to a variation in temperature between ca. 5 and 15°C at 2550 m altitude. A provisional land–sea correlation (Funza pollen–ODP Site 6778*O) is shown for the upper 1.2 Ma (Stages 3–35). Frequency analysis of several time series showed significant periods of the eccentricity (100 ka) and precession (23 and 19 ka) bands, showing orbital forcing and a strong change in climatic variability around 800 ka. At ca. 2.7 Ma, a significant cooling of ca. 5°C is documented, reflecting the classical terrestrial Pliocene–Pleistocene boundary, which correlates to the Reuverian–Praetiglian boundary of the NW European stratigraphical climatic subdivision.

INTRODUCTION

Long continental records of climatic change are scarce but are of great importance in facilitating the comparison of land-based and ocean-based climatic histories. In the Eastern Cordillera of Colombia, the high plain of Bogotá (ca. 25 × 40 km in size) represents the bottom of a former lake that occupied a subsiding intermontane basin (Fig. 1). After the final upheaval of the northern Andes between 5 and 3 Ma (van der Hammen *et al.*, 1973; Helmens, 1990; this volume), the development of a basin environment in the area of the present high plain of Bogotá started some 3.5 Ma (Helmens, 1990). Subsidence of the floor of the tectonic basin was more or less in equilibrium with sediment accumulation during most of the time and resulted in a sequence of almost 600 m of mainly lake sediments with an early fluvial influx. Pollen records have been retrieved from deep boreholes in these sediments. During periods with low lake levels in the central part of the basin, sediment accumulation ceased in the outer parts. This caused the presence of hiatuses in pollen records from the outer parts of the basin (van der Hammen and González, 1960, 1964).

The objective of this paper is to present an overview of the continuous history of vegetation development and climatic change during the last ca. 3 Ma, based on several research papers which have recently been published or are in press. Data are based on the deep boreholes Funza I (357 m) and Funza II (586 m) in the centre of the sedimentary basin, where sediments reach the greatest depth. The Funza II core, recovered in 1988, reached bedrock, indicating that the complete basin infill, representing Late Pliocene to latest Pleistocene, has been recovered.

Changes in the composition of the vegetation, which reflect climatic change, are documented by the pollen rain that is conserved in slowly accumulating lake sediments. Tropical mountains especially seem to be in a favourable position because climatic change results mainly in a vertical shift of vegetation belts over the mountain slopes (Fig. 2). The different vegetation belts stay in the vicinity of the lake and are registered continuously by their intercepted pollen. The sediments in the Bogotá basin, at 2550 m elevation, accumulated at an altitude that lies halfway between the highest position of the upper forest line (during interglacial conditions ca. 3500 m) and the lowest position of the upper forest line (during glacial conditions ca. 1800 m), rendering the Bogotá sediments a sensitive recorder of palaeoclimatic change.

SETTING OF PRESENT VEGETATION AND CLIMATE

The present-day altitudinal zonation of the vegetation in the Eastern Cordillera of Colombia (Fig. 2) is summarized in order to understand the changes documented by the pollen record. More complete accounts of the modern montane forest and paramo vegetation of the Colombian Andes are given in e.g. Cleef (1981), Cleef *et al.* (1983) and Cleef and Hooghiemstra (1984). The following vegetation zones can be recognized:

- tropical lowland rain forest from 0 to 1000 m: main taxa are *Byrsonima*, *Iriartea* and *Mauritia*
- subandean forest belt (lower montane forest) from 1000 to 2300 m: main taxa are *Acalypha*, *Alchornea* and *Cecropia*

FIG. 1. Map of Colombia and the area of the high plain of Bogotá in the Eastern Cordillera, indicating the topography of the surrounding mountains. (Redrawn after Andriessen *et al.*, 1993.)

— Andean forest belt (upper montane forest) from 2300 to 3200–3500 m: main taxa are *Podocarpus*, *Hedyosmum*, *Weinmannia*, *Quercus*, *Alnus*, *Vallea*, *Myrsine* (formerly *Rapanea*), *Symplocos*, *Ilex*, *Juglans*, *Miconia*, *Eugenia* and *Myrica*

— subparamo belt from 3200–3500 m to 3400–3600 m: main taxa are *Ericaceae*, *Hypericum*, *Compositae* and *Polylepis-Acaena*

— grassparamo belt from 3400–3600 m to 4000–4200 m: main taxa are *Gramineae*, *Valeriana*, *Caryophyllaceae*, *Gentianaceae*, *Plantago*, *Aragoa*, *Geranium*, *Ranunculus* and *Lycopodium* (species with foveolate spores)

— superparamo belt extending from 4000–4200 m upward: main taxa are *Draba*, mosses and blue algae

— nival zone proper, practically devoid of vegetation, extending from 4500–4800 m upward.

The highest areas of the Eastern Cordillera in the Sierra Nevada de Cocuy, some 200 km north of Bogotá, extending up to 5500 m, may be permanently covered by snow.

During glacial periods, lower temperatures caused a depression of the Andean vegetation belts, and a lowering of the position of the upper forest line of ca. 1200–1500 m has been seen (van der Hammen, 1974). The modern upper forest

line in the area of Bogotá at ca. 3200 m altitude corresponds with the ca. 9.5°C annual isotherm. Thus, temperature changes at the level of the high plain of Bogotá (2550 m; present-day average annual temperature 13–14°C) can be calculated when changes of the altitudinal position of the upper forest line are estimated on the basis of the pollen record, using a lapse rate of 0.66°C per 100 m displacement of the upper forest line.

ABSOLUTE TIME CONTROL OF THE SEDIMENTS OF THE BOGOTÁ BASIN

A revised geochronological framework for the sequence of unconsolidated sediments present in the Bogotá area was published recently (Andriessen *et al.*, 1993) to replace the original time frame of the Funza I pollen record (Hooghiemstra, 1984, 1989). This is based on 11 fission track datings on zircons that were obtained both from exposed ash layers and from a series of ashes from the Funza II core. The data 5.33 ± 1.02 Ma, 3.67 ± 0.50 Ma and 2.77 ± 0.50 Ma (Andriessen *et al.*, 1993) for sediments that are considered to have been deposited before, at the beginning

FIG. 2. Altitudinal distribution of vegetation belts in the Eastern Cordillera of Colombia at present and during the last glacial maximum. Vertical shifts of the vegetation belts are mainly related to changes in temperature. (Redrawn after Van der Hammen, 1974.)

and shortly after the final major upheaval of the Eastern Cordillera provide absolute chronological control for the older part of the sequence (6–2.5 Ma). Fission track data on zircon from the Funza II core (Fig. 3 and listed below) provide geochronological control for the younger part of the sequence (3–0 Ma) and these are coherent with the fission track dates of the older part of the sediment sequence:

- 67.7 m: 0.20 ± 0.12 Ma;
- 298–307 m: 1.02 ± 0.23 Ma;
- 317 m: 1.44 ± 0.33 Ma;
- 322 m: 1.01 ± 0.21 Ma;
- 506 m: 2.74 ± 0.63 Ma.

Nevertheless, three fission track dates on zircon, at 239 m

FIG. 3. Time control of the sediments of the Funza I and Funza II cores from the high plain of Bogotá (Colombia) based on fission track dates (after Andriessen *et al.*, 1993) on zircon from intercalated volcanic ash horizons of the Funza II core. Open circles indicate the control points of the graphical correlation between Funza I Arboreal Pollen% record and ODP Site 677 $\delta^{18}\text{O}$ record (Fig. 5). Solid circles indicate the estimated ages of the boundaries of the Funza II pollen zones (see Figs 11 and 12). For the upper part of the Funza II core, age estimations are based on a provisional correlation with the Specmap time scale (Imbrie *et al.*, 1984). For the lower part of the Funza II core, age estimations are based on a provisional visual correlation with the ODP Site 677 $\delta^{18}\text{O}$ record (Shackleton *et al.*, 1990).

FIG. 4. Graph of Funza I Arboreal Pollen percentages (*Alnus* included) versus time based on the revised time frame. Note the development of a distinct 100 ka climatic cycle (classical glacial-interglacial cycles) in the last ca. 0.8 Ma of the Quaternary. (After Hooghiemstra *et al.*, 1993.)

(0.26 ± 0.18 Ma), 250 m (0.27 ± 0.11 Ma) and 270–277 m (0.53 ± 0.15 Ma), are considered as too young (Fig. 3; see the discussion in Andriessen *et al.*, 1993).

LAND-SEA CORRELATION OF RECORDS OF CLIMATIC CHANGE

A challenging similarity between the climatic change, registered in Andean Colombian pollen records (Fig. 4), and the climate records in marine sediments is apparent. Graphical correlation of the Funza I Arboreal Pollen record with the $\delta^{18}\text{O}$ record of ODP Site 677 from the Eastern Pacific, by Shackleton and Hooghiemstra, is shown in Fig. 5. A set of 36 control points was established (Fig. 5; Hooghiemstra *et al.*, 1993). At present this 36-point model is considered the best estimate for a geochronological

framework for the upper part of the Funza sediment sequence. These control points, as well as the estimated ages of the pollen zone boundaries, based on provisional land-sea correlation, are graphed in Fig. 3. The intervals represented by Stages 3–25 show the best correlation between climatic oscillations.

The correlation procedure will be repeated when the temporal resolution of the Funza II core (at present ca. 5–6 ka; already for several intervals ca. 1 ka) is as high as that of the Funza I core (ca. 1 ka).

VARIABILITY OF QUATERNARY CLIMATIC CHANGE AND ORBITAL FORCING

The evolution of climatic variability has been studied in the interval of the Funza I pollen record that represents

FIG. 5. Graphical correlation of the Funza I Arboreal Pollen record (pollen data based on Hooghiemstra, 1984; time control based on Andriessen *et al.*, 1993) and $\delta^{18}\text{O}$ record ODP Site 677 (Shackleton *et al.*, 1990). Using the absolute time control of the Funza sediments and the ODP Site 677 $\delta^{18}\text{O}$ record, the intervals representing Stage 22 in both records and the core tops were correlated. Subsequently, the pollen record was minimally stretched and squeezed over 35 short intervals between 36 control points (indicated as triangles). The parallel records show the provisional correlation for $\delta^{18}\text{O}$ Stages 3–25. (After Hooghiemstra *et al.*, 1993; see also Hooghiemstra and Sarmiento, 1991.)

Arboreal pollen (Funza I pollen record)

FIG. 6. Frequency analysis (Maximum Entropy Spectrum Analysis) using the 'Arboreal Pollen' data set (*Alnus* included) of the Funza I core interval 2–340 m (period 30–1450 ka) by a 400-ka-wide window moving in 20 ka steps. This pollen data set represents the altitudinally shifting upper forest line, mainly as a response to temperature change. The first spectrum covers the interval 30–430 ka. Every fifth spectrum is shown bold, with spectral peaks identified by their corresponding period in ka. Some peaks are truncated for readability. Note the presence in the upper 29 spectra of the record periods of the eccentricity band (ca. 100 ka, representing the classical Quaternary glacial–interglacial cycles). A band which is related to the precession is continuously present in the record with periods centred at 21–24 and 17–19 ka. (After Melice in Hooghiemstra *et al.*, 1993.)

(using the revised time frame; Andriessen *et al.*, 1993) the period from 30 to 1450 ka (Hooghiemstra and Melice, 1991, 1993; Hooghiemstra *et al.*, 1993). The 1178 analysed pollen samples between 2.90 and 340.00 m core depth generate five time series with an average time resolution of ca. 1200 years. For this purpose a time frame is used, based on absolute datings (fission track datings on zircon; Andriessen *et al.*, 1993) in combination with correlation of the pollen record with the ODP Site 677 $\delta^{18}\text{O}$ record of the Eastern Pacific (Hooghiemstra *et al.*, 1993). This last procedure resulted in small downcore adjustments of the pollen record; in fact, the best possible corrections to compensate for changes in sediment accumulation rates. A set of 36 control points was generated (Hooghiemstra and Sarmiento, 1991; Hooghiemstra *et al.*, 1993).

The five different data sets (Arboreal Pollen, Arboreal Pollen excluding *Alnus*, *Alnus*, marsh elements and *Quercus*) represent different variables of the palaeoclimate (Hooghiemstra *et al.*, 1993). These time series were then analyzed by Melice in the frequency domain with the help of Maximum Entropy Spectrum Analysis and Thomson Multi-Taper Spectrum Analysis using a moving 400 ka window with steps of 20 ka. Frequencies closely related to the Milankovitch theory were detected in the five data sets. The presence of ca. 100,000 year periods (eccentricity band) was

found in time series with Arboreal Pollen and appeared to be restricted to the last ca. 800 ka (Fig. 6). Periodicities close to 23 ka (precession band) are present throughout the pollen record and are strongest in the data set of subparamo elements (Fig. 7). The five selected data sets reveal an evolution of orbital frequencies in the Middle and Upper Quaternary which is in general agreement with other marine (e.g. Imbrie *et al.*, 1984) and continental (e.g. Kukla *et al.*, 1990) records.

DEVELOPMENT OF FLORA AND VEGETATION OF ANDEAN MONTANE FORESTS AND PARAMO

Around 4–3 Ma, the principal upheaval of the area had ceased (van der Hammen *et al.*, 1973; Helmens, 1990; Andriessen *et al.*, 1993). The high plain of Bogotá was by then an extensive lake at approximately 2500 m altitude. In this lake basin, ca. 600 m of fluvial lacustrine and later pure lacustrine sediments were formed (Fig. 8), providing a long and continuous pollen record of the development of the montane vegetation belts and climatic change in northern South America during the Late Pliocene and Pleistocene time (Figs 9 and 10). Figure 9 shows the 357-m-long Funza I pollen record with a temporal resolution of ca. 1200 years (based on Hooghiemstra, 1984, 1989) representing the

subparamo elements (Funza I pollen record)

FIG. 7. Frequency analysis (Maximum Entropy Spectrum Analysis) using the data set of 'subparamo elements' of the Funza I core interval 2–340 m (period 30–1450 ka) by a 400-ka-wide window moving in 20 ka steps. The subparamo vegetation forms a belt with open (alpine) scrub vegetation above the upper forest line and is at present located from ca. 3200 to ca. 3500 m elevation (Fig. 2). The first spectrum covers the interval 30–430 ka. Every fifth spectrum is shown bold, with spectral peaks identified by their corresponding period in ka. Note the continuous presence of periods of the precession band (21–24 and 18–19 ka). (After Melice in Hooghiemstra *et al.*, 1993.)

interval from ca. 1.5 to 0.03 Ma. Figure 10 shows the upper 565 m of the Funza II pollen record with a temporal resolution of ca. 5000–6000 years (based on Hooghiemstra and Ran, *submitted* and Hooghiemstra and Cleef, *submitted*). Several phases in the development of montane forests and paramo vegetation of the Colombian Eastern Cordillera and distinct phases in the climate history can be recognized. In the next part, a concise account, based on the Funza II pollen record (depth intervals) and corroborated by the Funza I record, is given. Summary diagrams, upper forest line oscillations (temperature change) and provisional correlation with the marine $\delta^{18}\text{O}$ record is given in Fig. 11 for the interval 2–158 m (based on Hooghiemstra and Ran, *submitted*) and for the interval 205–540 m (based on Hooghiemstra and Cleef, *submitted*).

The interval 540–465 m core depth (3.2–2.7 Ma) shows that warm climatic conditions and pollen spectra have no Upper Quaternary analogues. The basin had just started to accumulate lacustrine and river sediments, after a period in which sediment only accumulated in the periferic valleys. The upper limit of the subandean forest belt was situated at some 500 m lower elevation than today. In the Andean forest belt *Podocarpus*-rich forest, *Hedyosmum*–*Weinmannia* forest (a precursor of the modern *Weinmannietum*) and

Vallea–*Miconia* forest, respectively, were the main constituents with increasing elevation. *Hypericum* and *Myrica* played an important part in the timberline dwarf forests, which possibly constituted a substantial transitional zone from the early Andean forest belt (upper montane forest belt) to the open grassparamo belt. The contribution of herbs to the paramo vegetation, dominated by Gramineae and Compositae, seems less diverse than during the Upper Quaternary. The Late Pliocene (upper) Andean forests were more open than during the Middle and Upper Quaternary, as heliophytic elements, such as *Borreria*, were abundant. The composition of forests on the high plain was subject to considerable change: arboreal taxa with pioneer qualities (*Dodonaea*, *Eugenia*) and other taxa (*Symplocos*, *Ilex*) constituted, seemingly at irregular intervals, azonal forests in the basin. The upper forest line oscillated most of the time from 2800 to 3600 m elevation. The average annual temperature on the high plain was 11.5–16.5°C.

The interval 470–460 m, dated around 2.7 Ma, shows a significant decrease in the contribution of Arboreal Pollen, suggesting that the average temperature level was lowered by some 4–5°C (provisional estimation). This episode of rapid cooling is followed by a period of gradually lowering temperatures, i.e. from 2.7 to 2.2 Ma (460–405 m core

FIG. 8. Lithology of the sediments from the Funza II bore hole (2–586 m core interval) in the basin of Bogotá. Descriptions are made by S.R. Arevalo-Gamboa and I.D. Pinzon-Villazon. (After Sarmiento-Perez, G., Ingeominas, Bogotá; internal document.)

FIG. 8. cont.

interval). This drop in temperature falls within the global period of transition; from the average warm Pliocene climates to the cold climatic conditions during the Lower Pleistocene. Indeed, the classical terrestrial Pliocene–Pleistocene boundary (Zagwijn, 1975, 1985, 1992) falls within the period which is characterized in the Funza record by cooling.

The interval 465–415 m core depth (2.7–2.2 Ma) shows colder climatic conditions. The upper forest line oscillated most of the time from 2600 to 2800 m in the first half of this period, and from 2400 to 2800 m in the second half. Average annual temperatures were 10.5–11.5 and 8.8–11.5°C, respectively. The *Podocarpus*-rich forest type occurred until the end of this period. *Weinmannia* was almost absent and *Hedyosmum* completely dominated, for the first time, the *Hedyosmum*–*Weinmannia* forest type. *Miconia* dominated in the *Vallea*–*Miconia* forest type, in which *Ilex*, *Myrsine* and *Daphnopsis* were probably associated elements. For the first time in the Pleistocene, paramo vegetation became

widespread in the Eastern Cordillera near Bogotá. Caryophyllaceae and *Valeriana* were the most dominant paramo herbs at that time, whereas the contribution of *Plantago* and *Aragoa* increased. During intervals with low water levels, marsh vegetation, including Cyperaceae, *Polygonum*, *Hydrocotyle*, *Ludwigia*, *Myriophyllum*, *Sphagnum* and *Azolla*, was abundant on the high plain.

The interval 415–337 m core depth (2.2–1.42 Ma) shows, for the first time in the record, a rather persistent cold climate. The upper forest line oscillated most of the time from 1900 to 2500 m, corresponding to an average annual temperature of 5.5–9.5°C on the high plain. *Podocarpus* had lost its dominant part in the (lower) Andean forest belt. *Hedyosmum*–*Weinmannia* forest and *Miconia*–*Vallea* forest were most important. *Daphnopsis* had almost disappeared from the Andean forest belt and *Borreria* became less common during this period, suggesting that forests became denser. *Hypericum* was, for the first time in the record, the most important element in the dwarf forest, but at the end of this period *Polylepis* dwarf forest started to increase near the upper forest line and lower paramo. *Juglans* appeared for the first time regularly with low frequency and *Styloceras* also became a more regular component of the Andean forest belt. On a local scale, *Plantago* became very abundant in the basin and probably replaced a great part of the local grassparamo.

The interval 337–257 m core depth (1.42–1.0 Ma) shows a long period with mainly cold climatic conditions. The upper forest line oscillated most of the time from 2200 to 2600 m, at the end of this period slightly increasing to 2400–2800 m. This corresponds to average annual temperatures on the high plain of 7.5–10 and 9–11.5°C, respectively. *Weinmannia* was almost absent in the Andean forest belt and a *Hedyosmum* forest, possibly with important contribution of *Eugenia*, *Myrsine* and Ericaceae, constituted a precursor of the present-day *Weinmannia* forest. *Vallea* contributed, for the first time in the record, of the same order as *Miconia* to the *Vallea*–*Miconia* forest type. *Borreria* occurred at low frequency and disappeared almost at the end of this period, indicating that the forest structure was more dense and unsuitable for heliophytic elements. *Polylepis* dwarf forest was important at the upper forest line, and in the (lower) paramo *Myrica* (*M. pubescens*) probably contributed substantially to the upper part of the Andean forest belt. The upper limit of subandean forest during this period reached higher elevations than during the lower part of the record (but only reached modern conditions after the immigration of *Quercus*, later on in the record). The lake on the high plain was shallow and extensive marsh prevailed during the first half of this period. Possibly due to tectonic adjustments of the basin, the lake became deeper from ca. 300 m core depth onward, and *Isoetes* vegetation and algae became abundant in short time.

The interval 257–205 m core depth (1.0–0.85 Ma) shows the first major glacial–interglacial cycles, characteristic of the Middle and Upper Quaternary. Comparison with the $\delta^{18}\text{O}$ record of the deep sea indicates that climatic change in the interval 240–205 m correlates with Stages 25–21. The interglacial (Stage 25) to glacial (Stage 22) lowering of the upper forest line is ca. 800 m (from 3000 to 1800 m, maximally), corresponding to a temperature decrease of

(C)

FIG. 8. cont.

(D)

FIG. 8. cont.

(E)

FIG. 8. Cont.

FIG. 9. Summary diagram of pollen record Funza I showing the altitudinally shifting vegetational belts in response to climatic change during the last ca. 1.5 Ma with an average time resolution of ca. 1200 years. Core depth (m) and age (ka) are indicated at the left hand side of the diagram. Indicated ages correspond to the control points of the correlation between Funza I Arboreal Pollen record and ODP Site 677 $\delta^{18}\text{O}$ record (see Fig. 5). For convenience, $\delta^{18}\text{O}$ Stage numbers 3–23 are indicated in the diagram based on a provisional correlation. Downcore oscillations in the representation of vegetation belts are shown for subandean forest belt, Andean forest belt, subparamo belt and grassparamo belt. The graph of downcore changes of the percentage of total Arboreal Pollen (AP; *Alnus* included) shows oscillations that, in fact, represent vertical shifts of the upper forest line over the mountain slopes as a response to mainly temperature change. Three percentage levels of AP are indicated that correspond to altitudinal positions of the upper forest line at 2000, 2550 and 3000 m. These levels, on which the boundary between interglacial and glacial periods is based, change to other percentages when new immigrants from the northern hemisphere, after crossing the Panamanian landbridge, changed the composition of the Andean montane forests. This happened at 257 m core depth (ca. 1 Ma), when *Alnus* immigrated into the area of Bogotá, and between 77 and 45 m when the contribution of zonal *Quercus* forest increased rapidly as a part of the Andean forest belt (*Quercus* immigrated into the area of Bogotá around 340 ka and appeared at ca. 94 m core depth in the Funza records). These changes in percentage levels are approximations to account for distinct changes in the composition of the Andean forest belt (percentage levels are not indicated in a short interval around 255 m core depth, which is characterized by a hiatus). Estimations are based on improved understanding of the Bogotá pollen records (Hooghiemstra, Ran, Van't Veer and Mommersteeg, unpublished data). The inferred changes in mean annual temperature, at the elevation of Bogotá, are from about 6 to 15°C. The former lake of Bogotá drained ca. 27 ka and this last part of the Quaternary is missing in the Funza records. The top samples are of Holocene age. (Pollen data after Hooghiemstra, 1984, 1989; time control after Andriessen *et al.*, 1993.)

FIG. 9. Cont.

FIG. 10. Summary diagram of pollen record Funza II (565–2 m core interval) for the period of ca. 3.2 Ma to ca. 27 ka, with a time resolution of ca. 5000–6000 years (sample distance 100 cm). Core depth (m) and estimated ages (ka) of pollen zone boundaries, based on absolute time control and land–sea correlation (Andriessen *et al.*, 1993), are indicated. In the interval 565–586 m, no pollen was recovered. For convenience, $\delta^{18}\text{O}$ Stage numbers 5–25 are indicated in the diagram based on a provisional correlation. Downcore oscillations in the representation of vegetation belts are shown for subandean forest belt, Andean forest belt, subparamo belt and grassparamo belt. The graph of downcore changes of the percentage of total Arboreal Pollen (AP; *Alnus* included) shows oscillations that, in fact, represent vertical shifts of the upper forest line over the mountain slopes as a response to mainly temperature change. (After Hooghiemstra and Cleef, *submitted*, and Hooghiemstra and Ran, *submitted*, for lower and upper parts of the pollen record, respectively.)

4.8°C. After the immigration of *Alnus*, a characteristic northern hemisphere genus, large areas of carr (swamp forest vegetation) developed on the wet flats around the lake, but *Alnus* probably also occurred incidentally as an element of the zonal forests. The contribution of *Myrica* was reduced considerably, indicating that *Myrica* contributed before to

the azonal vegetation (*M. parvifolia*) as well as to the zonal forests (*M. pubescens*). The large altitudinal shifts of all montane vegetation belts, in response to the main glacial–interglacial climatic cycles, in the remaining part of the record places the high plain alternately in the Andean forest belt and in the grassparamo belt.

FIG. 11. Correlation of the pollen records Funza I (Hooghiemstra, 1984, 1989) and Funza II (Hooghiemstra and Ran, *submitted*) and inferred climatic change for the interval of ca. 24–735 ka. Correlating pollen zones in both records have the same numbers, with a prefix F1 (Funza I) or F2 (Funza II). Depth and age of pollen zone boundaries are indicated. A provisional correlation with the marine $\delta^{18}\text{O}$ stratigraphy is indicated. Ages of $\delta^{18}\text{O}$ stages after Imbrie *et al.* (1984). (After Hooghiemstra and Ran, *submitted*.)

The interval 205–158 m is not recovered in Funza II due to technical problems (Fig. 10). This interval of the sediment sequence, however, is well documented in the Funza I core (Fig. 9). It corresponds to the interval of ca. 170–207 m of the Funza I core (Funza I pollen zones 27, 26 and 25A), representing the period of ca. 735–845 ka. This interval represents two distinct interglacial periods with a marked glacial in between and corresponds to the $\delta^{18}\text{O}$ Stages 21, 20 and 19 (Fig. 9). More precise fitting of this Funza II hiatus in the Funza I record is deferred until high temporal resolution pollen data are available. The upper forest line oscillated in this period, mainly from 3000 to 1900 m, for most of the time. The corresponding average annual temperature on the high plain is 13.6°C.

The interval 158–131 m core depth (estimated age 735–569 ka) shows warm climatic conditions most of the time and is tentatively correlated with the $\delta^{18}\text{O}$ Stages 19.1–15.1. The pollen spectra have no direct modern analogues because of the absence of *Quercus* and related conditions. The upper forest line oscillated mainly from 2100 to 2700 m for most of the time. The corresponding average annual temperature on the high plain is 6.5–11°C. The high plain was situated in the Andean forest belt most of the time. The upper limit of the subandean forest belt (*Acalypha*, *Alchornea*) was situated some hundreds of metres below the modern elevation. *Podocarpus* was most important in the lower part of the Andean forest belt. *Weinmannia* forest, the precursor of the modern *Weinmannietum*, included a substantial contribution of *Hedyosmum*, with lower frequency *Myrsine* and *Eugenia*. A type of *Vallea-Miconia* forest, including low presence of *Ilex* and *Myrsine*, could have occurred on the drier parts of the high plain. The lake was shallow most of the time, with local marsh vegetation of cyperaceous reed swamp and *Hydrocotyle*. *Myrica* thickets (*M. parvifolia*) and *Alnus* carr covered the wet flats around the lake. *Myrica* (*M. pubescens*) and *Alnus* possibly also contributed with low frequency to the zonal Andean forest belt. Dwarf forest of *Polylepis*, *Myrica* and Compositae scrub occurred at the upper forest line.

The interval 131–100 m core depth (estimated age 569–350 ka) shows cold climatic conditions most of the time and is tentatively correlated with the $\delta^{18}\text{O}$ Stages 14.4–11.1. The upper forest line oscillated mainly from 1800 to 2500 m. The corresponding average temperature on the high plain is 5–9.5°C. The high plain was situated in the grassparamo belt most of the time. Apart from Gramineae (e.g. *Calamagrostis*, *Chusquea*) and woody stem rosettes of *Espeletia* (Compositae), a variety of paramo herbs (*Valeriana*, Caryophyllaceae, *Geranium*, *Aragoa*, *Lycopodium* fov.) were present with substantial frequencies, and abundant cushion bogs of *Plantago* (*P. rigida*) were present. The water level in the lake was high and marsh vegetation limited. *Polylepis* dwarf forest occurred in the subparamo belt, along with shrub of Compositae, *Hypericum* and Ericaceae. In the Andean forest belt, *Vallea-Miconia* forest and *Weinmannia-Hedyosmum* forest were most important.

The interval 100–57 m core depth (estimated age 350–186 ka) shows warm climatic conditions most of the

time and is tentatively correlated with the $\delta^{18}\text{O}$ Stages 10.2–7.1. The upper forest line oscillated from 2000 to 2600 m in the first part and from 2600 to 2900 m in the last part of this interval. The corresponding average annual temperatures are 6–10 and 10–12°C, respectively. The high plain was, in the first part of this interval, mostly situated in the paramo and in the last part of this interval in the Andean forest belt. During this interval *Quercus* immigrated into the area of the high plain. *Quercus* forest occurred in a wide altitudinal range (1000–2800 m) and initially constituted local patches of forest, but at the end of this interval, zonal *Quercus* forests were a major part of the Andean forest belt. *Acalypha* and *Alchornea* reached higher elevations in the *Quercus* forests, and the upper limit of subandean forest rose to modern elevations. *Weinmannia* dominated in the *Weinmannia-Hedyosmum* forest type. At the end of this interval, the contribution of *Vallea-Miconia* forest increased markedly and replaced *Weinmannia* forest. *Podocarpus*-rich forest occurred in the lower part of the Andean forest belt. *Alnus* carr and vegetation of *Myrica* thickets were abundant around the lake, which was of a shallow type. Algae (*Botryococcus*) became very abundant from the beginning of this interval to the top of the record.

The interval 57–2 m core depth (estimated age 186–24 ka) shows, for the first time in the record, abundant presence of zonal *Quercus* forests. The composition of the Andean forest belt had changed dramatically. Based on Arboreal Percentages, climatic conditions seem warm most of the time, but the high frequency of *Quercus*, a wind-pollinated tree that produces large amounts of pollen, exaggerates natural conditions. This interval is provisionally correlated with the $\delta^{18}\text{O}$ Stages 6–3.0. The upper forest line oscillated from 2000 to 3000 m most of the time. The corresponding average annual temperature is 6–12.5°C. *Quercus* forests, resembling the modern *Saurauia-Quercus humboldtii* forest, and *Weinmannia-Hedyosmum* forest, resembling the modern *Weinmannietum*, dominated in the Andean forest belt. *Vallea-Miconia* forest probably resembled the modern *Xylosma-Duranta-Vallea* forest, but the latter is palynologically difficult to recognize. *Eugenia*, *Ilex* and *Myrsine* contributed substantially to this rather dry forest type of low stature. *Polylepis* dwarf forest was frequent at the forest line and possibly also in the paramo belt up to 4000 m. *Alnus* carr completely dominated the flat parts of the high plain. *Myrica* thickets and marsh vegetation were reduced in the last part of this period. Sediment accumulation was very high (up to 60 cm per 1000 years). Supposedly, erosion of the Tequendama Falls in the Rio Bogotá, the only outlet of the high plain, led to the final drainage of the lake, depending on the location between ca. 28 and 22 ka.

The Andean biozones IV–VII (van der Hammen *et al.*, 1973) are represented in the Funza records. Biozone IV (540–415 m core interval; estimated age 3.2–2.2 Ma) is mainly characterized by high percentages of *Borreria*. *Alnus* and *Quercus* are absent. In biozone V (415–257 m core interval; 2.2–1.0 Ma), *Polylepis* replaced *Hypericum* as the major element in the dwarf forest zone, *Weinmannia* replaced *Hedyosmum* as the most important element in the *Weinmannia-Hedyosmum* forests (precursor of the modern *Weinmannietum*), and the upper limit of the subandean forest

FIG. 12. Correlation of the pollen records Funza I (Hooghiemstra, 1984, 1989) and Funza II (Hooghiemstra and Cleef, *submitted*) and inferred climatic change for the interval 0.8 to ca. 3.2 Ma. Correlating pollen zones in both records have the same numbers, with a prefix F1 (Funza I) or F2 (Funza II). Depth and age of pollen zone boundaries are indicated. A provisional correlation with the marine $\delta^{18}\text{O}$ stratigraphy is indicated. Ages of $\delta^{18}\text{O}$ stages after Imbrie *et al.* (1984) up to Stage 22 and after time control of ODP Site 677 (Shackleton *et al.*, 1990) for the lower part of the pollen record. (After Hooghiemstra and Cleef, *submitted*.)

belt had increased several hundreds of metres. *Alnus* and *Quercus* are still absent. Biozone VI (257–94 m core interval; estimated age 1.0–0.33 Ma) is characterized by the immigration of *Alnus* (first appearance date for the study area 1.0 Ma). Biozone VII (94–0 m core interval; estimated age 0.33 Ma to recent) is characterized by the immigration of *Quercus* (first appearance date for the study area 0.33 Ma, but present as an element that formed relevant zonal forests

since 0.2 Ma). The upper limit of the subandean forest belt increased and reached modern elevations.

CONCLUSIONS

The extremely thick sediment sequence of the high plain of Bogotá, which accumulated continuously during the last 3 Ma, forms a unique and important source of data for

palaeoclimatological, palaeoecological and biogeographical studies with high temporal resolution. The first studies were initiated by van der Hammen and the present research is characterized by interdisciplinary studies. Several research projects concerning different aspects of the Quaternary history of the high plain of Bogotá are in progress. They are carried out within the research tasks of the PAGES Project of IGBP (International Geosphere-Biosphere Programme); see IGBP Global Change Reports 12 (1990) and 16 (1991).

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