

Pollen- and diatom based environmental history since the Last Glacial Maximum from the Andean core Fúquene-7, Colombia

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ABSTRACT: The late Pleistocene–Holocene ecological and limnological history of Lake Fúquene (2580 m a.s.l.), in the Colombian Andes, is reconstructed on the basis of diatom, pollen and sediment analyses of the upper 7 m of the core Fúquene-7. Time control is provided by 11 accelerator mass spectrometry (AMS) ¹⁴C dates ranging from 19 670 ± 240 to 6040 ± 60 yr BP. In this paper we present the evolution of the lake and its surroundings. Glacial times were cold and dry, lake-levels were low and the area was surrounded by paramo and subparamo vegetation. Late-glacial conditions were warm and humid. The El Abra Stadial, a Younger Dryas equivalent, is reflected by a gap in the sedimentary record, a consequence of the cessation of deposition owing to a drop in lake-level. The early Holocene was warm and humid; at this time the lake reached its maximum extension and was surrounded by Andean forest. The onset of the drier climate prevailing today took place in the middle Holocene, a process that is reflected earlier in the diatom and sediment records than in the pollen records. In the late Holocene human activity reduced the forest and transformed the landscape.

Climate patterns from the Late-glacial and throughout the Holocene, as represented in our record, are similar to other records from Colombia and northern South America (the Caribbean, Venezuela and Panama) and suggest that the changes in lake-level were the result of precipitation variations driven by latitudinal shifts of the Intertropical Convergence Zone. Copyright © 2003 John Wiley & Sons, Ltd.

KEYWORDS: lake-level change; palaeoecology; diatoms; pollen; late Pleistocene; Holocene; climatic change; Eastern Cordillera; Colombia.

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Introduction

Fluctuations in lake-level and water chemistry roughly correspond to long-term changes in the balance between precipitation and evaporation, which in turn, may be interpreted in terms of climate variability. Long-term changes in precipitation at these near-equatorial latitudes is generally ascribed to shifts in the average position of the Intertropical Convergence

Zone (ITCZ) forced by the 21 000 yr precession cycle. Martin *et al.* (1997) and Haugh *et al.* (2001) postulated that during the early Holocene (12 400 to 8800 cal. yr BP—10 500 to 7500 extrapolated ¹⁴C ages—and 11 500 to 5400 cal. yr BP, respectively), the increase in precipitation recorded for northern South America was the result of a more northerly position of the ITCZ during the Northern Hemisphere summer. In the late Holocene, the average position of the ITCZ shifted southwards, decreasing precipitation during summer in the northern part of South America (Haugh *et al.*, 2001).

The littoral location of the core Fúquene-7 makes it a particularly sensitive register of changes in the local flora and aquatic plants as a result of changes in water level. Other cores from Lake Fúquene have been studied palynologically: core Fúquene-1 covers the period of ca. 27 000 ¹⁴C yr BP to recent (Van Geel and Van der Hammen, 1973), core Fúquene-2 records the period of ca. 32 000 ¹⁴C yr BP to recent (Van Geel and Van der Hammen, 1973), core Fúquene-3 records

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the period of ca. 125 000 yr BP to present (Van der Hammen and Hooghiemstra, 2002), and core Fúquene-7 represents the past ca. 70 000 yr BP (Mommersteeg, 1998).

Up to now, water levels of Colombian lakes have been reconstructed on the basis of inferred competition among plant taxa from wet lake shores, shallow water and deep water. Such a registering system may be quite accurate when the lake shore is close to the coring site. However, in large lakes where coring sites are located far from the shore this monitoring mechanism is less accurate. Van 't Veer and Hooghiemstra (2000) identified five aquatic pollen taxa as indicators of water depth. From deep to shallow water these taxa are: *Isoetes*, Cyperaceae, *Hydrocotyle*, *Ludwigia* and *Myriophyllum*. Other taxa indicative of lake levels (Hooghiemstra, 1984) are *Rumex*, *Polygonum*, *Typha*, *Sagittaria*, *Utricularia*, Compositae (e.g. *Bidens*; see Van 't Veer *et al.*, 2000) and *Plantago* (see e.g. Bosman *et al.*, 1994). Low water levels may expose organic material, providing the opportunity for fungi to start the process of decomposition (see Bosman *et al.* (1994) on fungi as possible depth indicators). Finally, shrubs and trees characteristic of swampy and poorly drained soils around lakes, such as *Myrica* and *Alnus*, can be used to infer lake-level changes (Hooghiemstra, 1984; Mommersteeg, 1998).

Other papers focused on lake-level reconstructions are the studies of Laguna Verde (Kuhry, 1988) and Van der Hammen and González (1960) on Laguna La America. Van 't Veer *et al.* (2000) described lake-level changes during the El Abra Stadial of Colombia, which is claimed to be the equivalent of the Younger Dryas climate oscillation (Van der Hammen and Hooghiemstra, 1995).

In this paper we take a further step by studying diatoms and magnetic minerals. Diatoms are excellent palaeoindicators of lake-level fluctuations and changes in water chemistry, and magnetic minerals are used to infer erosion in the lake hinterland. When integrating palynological and diatom analyses, we demonstrate that although their results are similar, diatoms record earlier changes in water volume, hence the importance of combining different proxys when interpreting climate records.

Environmental setting of Lake Fúquene

Geography and climate

Lake Fúquene (5°27'N, 73°46'W) is located in the Eastern Cordillera of Colombia at 2580 m above sea-level (Fig. 1). The present lake is the remnant of a larger Pleistocene lake that covered the Ubaté-Chiquinquirá high plain. Maximum thickness of the lacustrine sediments in the Fúquene basin is unknown; however the longest core recovered up to now is the 43-m-deep core Fúquene-3 (Van der Hammen and Hooghiemstra, 2002) that represents the last ca. 124,000 yr BP. The area of the present lake is 35 km²; it is 8 km long, 4 km wide and for the most part between 2 and 5 m deep (Mommersteeg, 1998), with seasonal fluctuations of about 1 m (Van Geel and Van der Hammen, 1973; Mommersteeg, 1998). There are several rivers and creeks that empty into the lake; Río Suarez is its only outlet (Donato *et al.*, 1987).

The annual migration of the ITCZ controls the modern precipitation regime in the region. There are two rainy seasons and two dry seasons. The dry periods are from December to February and from June to August, and the rainy seasons are from March to May and from September to November (Eidt, 1952). Monthly precipitation ranges from ca. 36 mm

to 208 mm, with minimum and maximum values of 0 mm and 699 mm, respectively. Owing to the shallowness of Lake Fúquene, minor changes in net precipitation result in significant fluctuations of the lake-level (Mommersteeg, 1998). The region is relatively isothermic during most of the year because of its location at low latitude and the stabilising presence of large water bodies (lakes Fúquene and Cucunubá; Eidt, 1952). Average annual temperature is about 13° to 14 °C, but the daily temperature range is wide and night frost may even occur during the dry periods (Van Geel and Van der Hammen, 1973).

Regional and local vegetation

The gradient in precipitation and altitude in the Fúquene basin allows the simultaneous presence of dry montane forest (500–1000 mm annual precipitation) and wet montane forest (1000–2000 mm annual precipitation) (Van Geel and Van der Hammen, 1973). Floristic surveys of remnants of original vegetation in a wide area around Lake Fúquene are available (e.g. Cleef, 1981; Cleef and Hooghiemstra, 1984), as are calibrations of pollen records based on the relationship between modern vegetation and modern pollen rain (Van der Hammen and González, 1960, 1963; Grabandt, 1980, 1985; Melief, 1984; Van 't Veer and Hooghiemstra, 2000). The major taxa of these vegetation belts are given below; the majority of them were recognised in the pollen spectra of core Fúquene-7.

The subandean (or lower montane) forest belt is present from 1000 to 2300–2500 m altitude. Annual precipitation is 1500–2700 mm; mean annual temperature ranges from 19° to 23 °C in the lower zones, and from 14° to 19 °C in higher altitudes. The main floristic elements are *Acalypha*, *Alchornea* and *Urticaceae/Moraceae*.

The Andean (or upper montane) forest belt is present from 2300–2500 to 3200–3500 m altitude. Annual precipitation is 700–1400 mm in the dry interandean valleys and 1000–3000 mm on the outer slopes; mean annual temperature ranges from 9° to 16 °C. The main floristic elements are *Alnus*, *Cedrela*, *Clethra*, *Daphnopsis*, *Dodonaea*, *Eugenia*, *Hedyosmum*, *Ilex*, *Juglans*, *Miconia*, other Melastomataceae, *Myrica*, *Myrsine* (= *Rapanea*), other Myrtaceae, *Podocarpus*, *Polylepis*, *Quercus*, *Symplocos*, *Vallea* and *Weinmannia*. The upper forest line is located at about 3200 m altitude; arboreal taxa such as Melastomataceae, *Polylepis*, *Quercus* and *Weinmannia* may be dominant in these ecotone forests.

The subparamo belt is present from about 3200–3500 to 3500–3700 m altitude. Annual precipitation is 700–2500 mm; mean annual temperature ranges between 6° and 9 °C. The main floristic elements are *Hypericum*, Ericaceae (which cannot be identified to the generic level but include important genera such as *Befaria*, *Gaultheria*, *Gnaphalium*, *Macleania*, *Pernettya* and *Vaccinium*) and Compositae (which cannot be identified to the generic level either, but include important genera such as *Baccharis*, *Diplostegium*, *Espeletia*, *Oritrophium* and *Senecio*).

The grassparamo belt is present from 3500–3700 m to 4200–4300 m altitude. Annual precipitation is 700–2500 mm; mean annual temperature is 3–6 °C. The main floristic elements are Gramineae (which cannot be identified to the generic level but include important genera such as *Agrostis*, *Calamagrostis*, *Festuca*, *Muehlenbergia* and *Swallenochloa*) and a number of shrubs and herbs such as *Aragoa*, *Gernanium*, *Halenia*, *Loricaria*, *Lupinus*, *Lysipomia*, *Paepalanthus*, *Plantago*, *Puya*, *Rhizocephalum* and *Valeriana*.

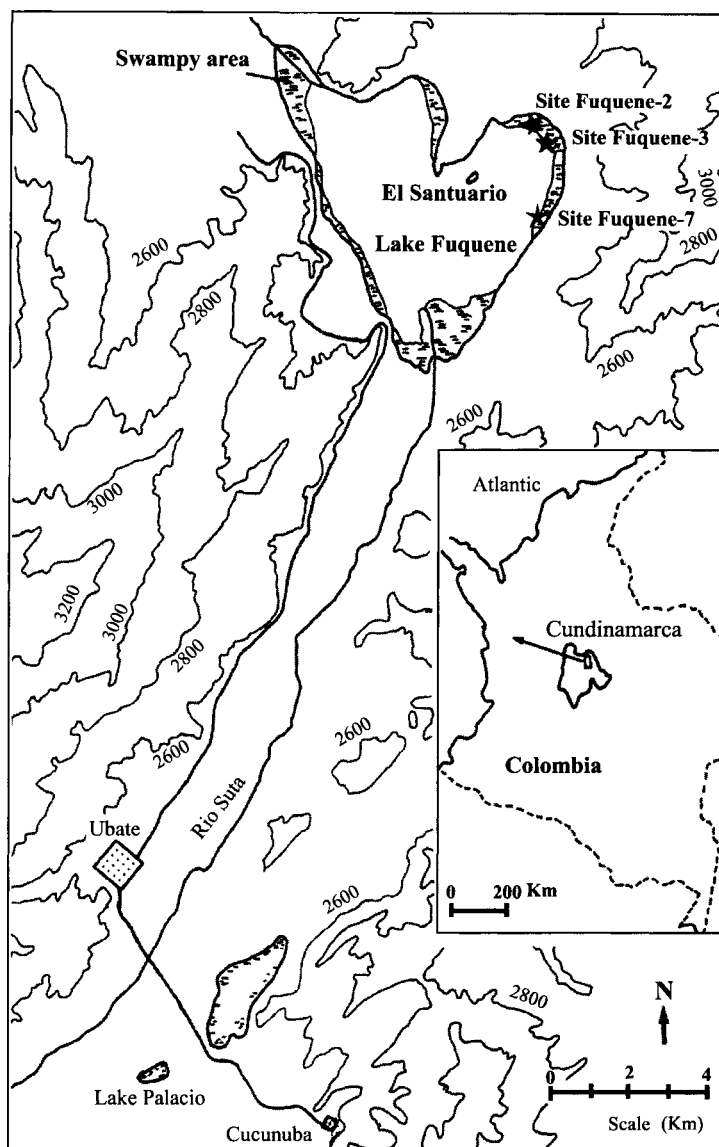


Figure 1 Map showing the location of Lake Fúquene in the Eastern Cordillera of Colombia and the coring sites for Fúquene-2, Fúquene-3 and Fúquene-7. The geographical position of this map is indicated on the inset figure by the small rectangle in the province of Cundinamarca, in the centre of Colombia. Figure modified after Van der Hammen and Hooghiemstra (2002)

The superparamo belt is present from about 4200–4300 m to the perennial snow cap. Species of Caryophyllaceae (such as *Arenaria*, *Cerastium*) and Cruciferae (*Draba*), mosses and cyanobacteria are characteristic. The vegetation cover is incomplete owing to night frost, creeping soil, and mechanical damage to vegetation by downslope chutes of rocks and boulders.

Lakes in the Andean forest belt, and in the paramo belt in particular, may often have *Isoetes*, *Azolla*, *Ludwigia*, *Potamogeton* and *Myriophyllum*, with *Polygonum*, *Typha* and *Carex* reedswamp occurring around the margins.

The altitudinal zonation of the vegetation belts is largely determined by the mean annual temperature: the upper forest line corresponds to the 9.5°C annual isotherm. The gradient of change in temperature is some 0.6°C 100 m⁻¹ vertical displacement, but as high as ca. 0.78°C 100 m⁻¹ during dry glacial conditions (Wille *et al.*, 2001). Changes in mean annual precipitation have little impact on temperature reconstructions (Van der Hammen and González, 1960, 1963; Hooghiemstra, 1984) and their contribution is estimated on the basis of the forest composition and lake-level status. Recent research suggests that low atmospheric *p*CO₂ during a glacial stage may cause the position of the upper forest line to be lower than it is

under present-day *p*CO₂ values, independent of temperature (Boom *et al.*, 2001, and references therein). This effect cannot be quantified yet and may be compensated for by a steeper glacial lapse rate (see the discussion in Wille *et al.*, 2001).

Water chemistry

Lake Fúquene is currently enriched with nutrients through runoff carrying fertilisers and extra sediments as a consequence of human activities in the catchment area. Once in the lake, water is retained between 6 to 9 months (CAR, 1974a; CARb, 1974 in Donato *et al.*, 1987). Water chemistry in the lake is strongly influenced by ground water, springs and local aquifers rich in HCO₃, Cl, SO₄ and Mg, and its hardness, often indicated by the concentration of the calcium ion, oscillates between 22 and 3000 ppm (De Speelman (1982) in Donato *et al.*, 1987). The north–south orientation of the lake and its valley and the shallowness of the lake favour the impact of the trade winds, which prevent the waters from stratifying (Donato *et al.*, 1987). Water turbulence leads to some resuspension of minerogenic material and nutrients. The thermocline and nutriclines are

only ephemeral limnological features, i.e. epilimnion and hypolimnion are seldom well-established.

Methods

Core recovery, pollen analysis and time control

The 14-m long Fúquene-7 core was drilled in the north-east margin of the lake using a hand-operated Dachnovsky corer. The sediment cores were transported to Amsterdam and stored in a dark cold room. Pollen samples were collected at 5-cm intervals along the core. Standard preparation techniques (Faegri and Iversen, 1975) were applied, including treatment with 10% KOH, natriumpyrophosphate, HCl (10%) and acetolysis mixture following Erdtman (1960). Gravitational separation was applied with a bromoform alcohol mixture. Finally the samples were mounted with glycerine jelly. Pollen concentration values were calculated by adding a known number of *Lycopodium* spores to each sample. About 300 pollen grains were counted per level. The pollen sum includes the following ecological groups: subandean forest, Andean forest, subparamo, grassparamo and superparamo. *Alnus* was excluded from the pollen sum as it represents mainly azonal swamp forest on wet soils around the lake (Hooghiemstra, 1984). Representation of lake shore taxa, shallow water taxa and deep water taxa is expressed on the pollen sum. The software TILIA and TILIAGRAPH were used to calculate percentages and to construct the pollen diagram. For more details concerning pollen analysis see Mommersteeg (1998).

Accelerator mass spectrometry (AMS) radiocarbon dates were obtained from 11 bulk samples of organic-rich clay for time control (Mommersteeg, 1998; Van 't Veer *et al.*, 2000) (Table 1). For depths above 349 cm a linear extrapolation of radiocarbon dates was used.

Diatom analysis

We collected 52 samples for diatom analysis at 20-cm intervals along the core. Diatoms were extracted from the sediments by standard procedures (Battarbee, 1986). Permanent slides were mounted in Naphrax, r.i. 1.70 and examined at 1000 $\times$ magnification with an Olympus BX40 microscope. A minimum of 400 valves were counted per slide. The software TILIA and TILIAGRAPH were used to calculate percentages and to construct the diatom diagrams. Detrended correspondence analysis (DCA) was carried out using CANOCO (Ter Braak,

1986). Samples between 215 and 248 cm depth did not contain diatoms and were excluded. Forty samples yielded good quality results. 'Calibrate' version 0.82 (Juggins, 1998) based on the modern diatom data base of Gasse *et al.* (1995) was used to reconstruct pH and conductivity. We recorded 51 diatom species, of which 36 were present in the African data set. As the matching percentage between all diatom spectra of our record and the diatom taxa present in the calibration set was above 70% on average, the reconstructed pH and conductivity for Fúquene can be accepted with confidence. The interval between 99 to 120 cm had low percentages of matches of about 32%, therefore we did not trust the reconstructed pH and conductivity at that interval (see later). We used the following literature for the diatom identification and ecological interpretations: Germain (1981), Patrick and Reimer (1966), Krammer and Lange-Bertalot (1986, 1991) and Gasse (1980, 1986).

Magnetic minerals

In total 36 samples of wet sediment—taken at 20-cm intervals along the core—were used to gauge mineral magnetic properties. Samples were magnetised in a magnetic field at room temperature. Saturation isothermal remnant magnetisation (SIRM) readings were taken for each sample. The SIRM value indicates the level at which 'isothermal remnant magnetisation' (IRM) stabilises, independently of the increases of the magnetic field. According to Lowe and Walker (1997), IRM is the magnetic moment activated and retained by a sample placed in a magnetic field at room temperature.

Interpretation and comparison of the proxy records

Fluctuations in lake-level were inferred from the pollen and the diatom records. Ecological ranges of diatoms were obtained from the publications listed above. Dominance of littoral and planktonic diatoms were indicative of low and high lake-levels, respectively. Changes in pH—as reflected in the diatom assemblages—are indicative of the interaction between spring waters, local input of aquifers and the volume of the lake. The record of pollen-based lake-level changes (Mommersteeg, 1998, Van 't Veer *et al.*, 2000) was visually compared with the diatom-based record of lake-level oscillations. The regional vegetation history of the Fúquene area is taken from Mommersteeg (1998) and is based principally on the record of altitudinal shifts of the upper forest line. Changes of magnetic mineral concentration were used to infer rates of erosion: high concentrations represent periods of increased sedimentation (or soil erosion) whereas low concentrations reflect reduced sedimentation (Lowe and Walker, 1997).

Results and interpretation

Stratigraphy of the core

The following sedimentary sequence was observed in the core:

- 0–25 cm Grey clay matrix with detrital material.
- 25–275 cm Black organogenic material (peat).
- 275–700 cm Dark brown clay matrix with organic and detrital material intercalated with grey sediments of silt and fine sand at 350–360, 375, 440–450, 515–520, 547 and 550 cm.

Table 1 List of radiocarbon dates of core Fúquene-7 (after Mommersteeg, 1998)

Depth (cm)	AMS ^{14}C age
349–350	6040 $\pm$ 60
403–404	7070 $\pm$ 50
448–449	7780 $\pm$ 60
467–468	7850 $\pm$ 70
481–482	7890 $\pm$ 60
491–492	7970 $\pm$ 60
504–505	8680 $\pm$ 60
521–522	13 110 $\pm$ 120
543–544	14 200 $\pm$ 120
651–652	17 990 $\pm$ 60
699–700	19 670 $\pm$ 240

Analysis of diatoms and other proxies

Diatoms growing in the lake today include *Cyclotella bodanica*, *Aulacoseira granulata*, *A. italica*, *Fragilaria construens*, *Tabellaria flocculosa*, *Navicula capitata*, *N. rhynchocephala*, *Navicula* sp., *Cymbella ventricosa*, *Gomphonema parvulum* and *Epithemia zebra* (Donato *et al.*, 1987). Samples collected in January 2000 showed that in the littoral zone *Fragilaria* spp. and *Tabellaria flocculosa* are dominant, whereas the surface sediments in the centre of the lake are dominated by *Epithemia sorex*, *Fragilaria* spp. and *Aulacoseira distans*. Good analogues for fossil assemblages are difficult to find owing to the pollution of the lake water.

Down-core changes in the diatom assemblages are shown in Fig. 2. The records of SIRM, reconstructed pH and conductivity, and the record of lake-level changes are presented in Fig. 3. Some aspects of the reconstructed pH and conductivity are discussed below.

The similarity between the curve of the first axis of the DCA analysis (eigenvalue of 0.666) plotted against depth, and the pH obtained from 'Calibrate' (Fig. 4), suggests that pH could be the main chemical variable determining the distribution of the diatoms in the record. For the interval from 99 to 120 cm, 'Calibrate' indicates a maximum pH of 8. However, the low match in 'Calibrate' (about 32%) for this interval and the dominance of *Aulacoseira distans* cf. *laevissima* suggest that the pH was around 6.8 (E. Haworth, personal communication, 2000; Gasse, 1986). The conductivity for the interval of 99 to 120 cm was probably lower than the value obtained from 'Calibrate', as suggested again by the presence of *A. distans* cf. *laevissima*, which inhabits environments of low to very low conductivity ($<300 \mu\text{S cm}^{-1}$; E. Haworth, personal communication).

The most conspicuous relationships between pH and diatom assemblages are seen in zone 1 (Figs 2 and 3), where high pH corresponds to the dominance of *F. pinnata* and *F. brevistriata*, and zones 2 to 6, where lower pH values correspond to the dominance of *C. stelligera* and *A. ambigua* assemblages. The marked change in assemblage composition, pH and conductivity at about 550 cm core depth reflects an important reorganisation of the lake hydrology, as discussed below.

Description of the diatom record

Diatom zonation was based on visual inspection of the percentage diagram and determined according to changes in dominance of certain taxa ($>50\%$ of the total valves counted per depth). The ecological ranges of the diatom species are presented in Table 2. We recognise the following seven zones (FUQ-1 to FUQ-7).

Zone FUQ-1 (699–550 cm; estimated period from 19 700 to ca. 14 200 ^{14}C yr BP) is dominated by the genus *Fragilaria*, in particular *F. brevistriata* (40–60%) and *F. pinnata* (30–45%). Average sedimentation rate is about 29 cm kyr^{-1} . Magnetic minerals peak at 555 cm depth and decrease rapidly to remain relatively low. This zone includes radiocarbon ages of $19\,670 \pm 240$ ^{14}C yr BP at 699 cm, and $17\,990 \pm 60$ ^{14}C yr BP at 651 cm.

Zone FUQ-2 (550–510 cm; estimated period from ca. 14 200 ^{14}C yr BP to ca. 8680 ^{14}C yr BP) is dominated by *F. pinnata* (60%) followed by *F. construens* (10%). *Fragilaria brevistriata* decreases to 5–10% relative to the lower zone. New elements, such as *Cocconeis placentula*, *Gomphonema truncatum*, *Navicula radiosa* and *Epithemia turgida* appear in this zone. *Aulacoseira ambigua* starts to increase. The average

sedimentation rate changes from 29 cm kyr^{-1} at the bottom to 4 cm kyr^{-1} at the top of the zone. At the top of the zone between ca. 521 and 504 cm, radiocarbon dates indicate a gap in the sediment record.

Zone FUQ-3 (510–410 cm, estimated period ca. 8680 to ca. 7070 ^{14}C yr BP) shows a conspicuous increase in *Aulacoseira ambigua* (70–75%), particularly at the beginning and at the end of the zone, and a decrease in *Fragilaria* spp. Other common diatoms are *Cymbella microcephala*, *Epithemia turgida*, *Achnanthes minutissima* and *Navicula minuscula* var. *muralis*, which increase between 460 and 440 cm. At the beginning of the zone the sedimentation rates are high and concentrations of magnetic minerals are low. At the top of the zone the concentration of magnetic minerals increases and sedimentation rates start to decrease.

Zone FUQ-4 (410–248 cm, estimated period from ca. 7070 to 4300 ^{14}C yr BP) shows a dominance of *A. ambigua* and *Cyclotella stelligera*. Along with the dominant *A. ambigua*, there are also *Cymbella microcephala*, *Gomphonema angustatum* and *Nitzschia amphibia*. At the beginning of the zone the concentrations of magnetic minerals are the highest in the entire core; in the middle and upper part of this period values are minimal.

Zone FUQ-5 (248–215 cm, estimated period from ca. 4300 to 3700 ^{14}C yr BP based on extrapolation of radiocarbon dates) features an absence of diatoms except for some corroded valves of *Fragilaria* spp., *Aulacoseira* spp., *Cyclotella* spp. and *Brachysira* sp. Concentration of magnetic minerals is low.

Zone FUQ-6 (215–90 cm, estimated period from ca. 3700 to 1600 ^{14}C yr BP age based on extrapolation of radiocarbon dates) is dominated by *Cyclotella stelligera* and *Fragilaria brevistriata* at the bottom, whereas *A. distans* cf. *laevissima* and *Brachysira brebissonii* dominate at the top. There are low percentages of *A. ambigua*, *F. pinnata*, *B. brebissonii*, *C. stelligera* and *F. construens*. The low values of magnetic minerals of the zone below are maintained.

Zone FUQ-7 (90–0 cm, ca. 1600 ^{14}C yr BP to recent, age based on extrapolation of radiocarbon dates) is dominated by *Cyclotella stelligera* and *Aulacoseira ambigua*. Common diatoms are *Gomphonema gracile*, *Brachysira brebissonii*, *Aulacoseira granulata* var. *angustissima*, *Aulacoseira crenulata*, *Cymbella silesiaca*, *Cymbella gracile*, *Brachysira vitrea*, *Eunotia serra* var. *serra*, *Eunotia soleirolii*, *Eunotia flexuosa*, *Tabellaria flocculosa*, *Fragilaria construens* and *Synedra ulna*. The concentration of magnetic minerals is still very low.

Interpretation of the diatom record

The dominance of littoral (*Fragilaria* spp) diatoms during the period from 19 700 to ca. 14 200 ^{14}C yr BP (FUQ-1) suggests that the lake was shallow at the time. The pH ranged between 7.6 and 7.8. The conductivity shows a decrease from $250 \mu\text{S cm}^{-1}$ at the bottom to $170 \mu\text{S cm}^{-1}$ at the top. There is an increase of epiphytic, aerophilous and planktonic diatoms at ca. 14 200 ^{14}C yr BP (FUQ-2). Their increase may indicate an increase or decrease in the lake-level (i.e. an increase in lake-level would increase the extension of the lake and hence of the littoral area available those diatoms to colonise; a decrease in lake-level would cause the littoral area to be closer to the coring site, and hence to cause an increase in the proportion of those diatoms in the samples). However, on the basis of the increase in the planktonic *Aulacoseira ambigua* and of the fact that the epiphytic and aerophilous diatom species are highly represented during high lake-levels (see FUQ-3 and FUQ-4), we conclude that the lake-level started to increase (rather than



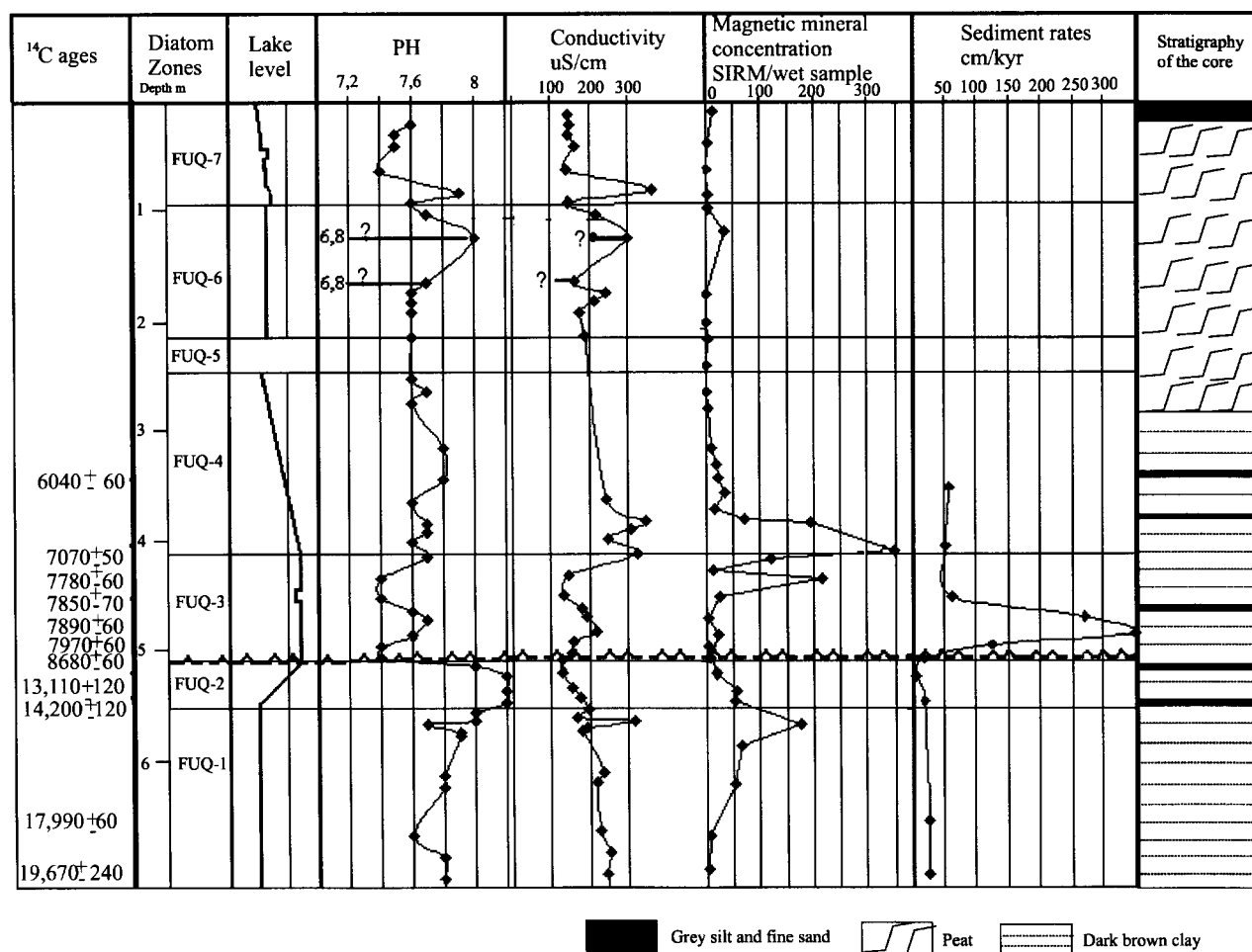


Figure 3 Limnological reconstruction of Lake Fúquene based on diatom analysis. From left to right: radiocarbon ages, diatom zones, inferred lake-level changes, reconstructed pH and conductivity, record of magnetic mineral concentration, sedimentation rates and lithology of the core

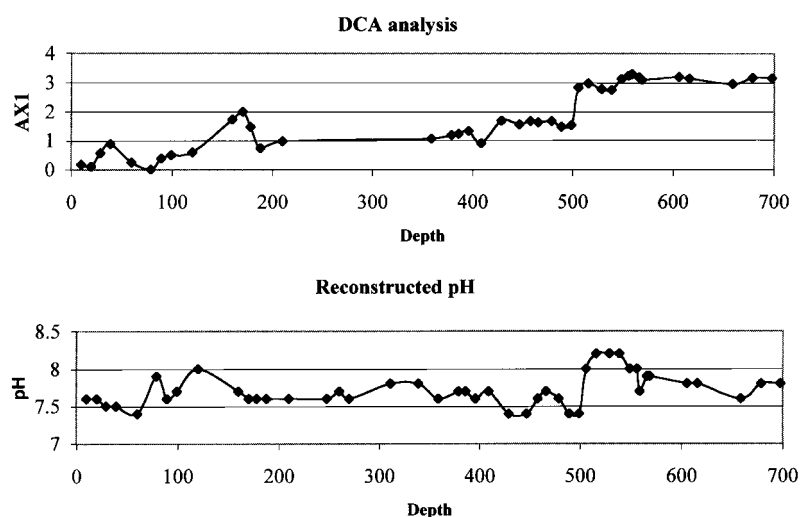


Figure 4 Comparison between results from detrended correspondence analysis (DCA) and reconstructed pH

decrease) ca. 14 200 yr BP. The decline in magnetic mineral concentration suggests a decrease in erosion, probably as a consequence of an increase in lake-level and/or vegetation cover. The pH reaches 8–8.2 at the time of the increase in lake-level. This period is followed by a gap in the sediment record; the period from ca. 13 110 to ca. 8680 ^{14}C yr BP is not represented.

The diatom zone FUQ-3 is dominated by planktonic *A. ambigua*; the relative increase of other planktonic species, and

the decrease in littoral species suggest that the lake reached its maximum extension. However, an increase in epiphytic and littoral species along with a decrease in planktonic taxa at ca. 7780 ^{14}C yr BP suggest a temporary decrease in lake-level. During this period the pH values decreased from 8.2 (zone below) to 7.4, suggesting a major influence of runoff and local aquifers into the lake carrying more acidic water owing to dissolution of CaCO_3 and oxidation of Fe_2S from the surrounding rocks (Caruccio and Geidel, 1978). Both minerals

Table 2 List of diatom taxa found in the Fúquene-7 core and their ecological preference. Abbreviations: L, littoral; e, epiphytic, or associated with floating masses of aquatic plants, or growing on the surface of various types of filamentous algae; b, benthic—taxa that live attached to hard substrates or fine-grained sediments; c, crenophytic; a, aerophylous; p, planktonic: free floating; O, oligohalobous: taxa that need salt concentrations <0.2‰; m, mesohalobous—taxa that need salt concentrations of 0.2–30‰; e, euhalobous: Hf, halophobous—taxa that cannot tolerate even slightly salty water; Ac, acidophilous—taxa that occur at values just below pH 7, but widest distribution occurs at pH < 7; I, indifferent or circumneutral, occur near a 7 pH value; Af, alkaliphilous—taxa that occur at values just above pH 7, but widest distribution occurs at pH > 7; Ab, alkalibiontic—taxa that require pH > 7

Species	Habitat					Salinity				pH			
	L	e	b	a	p	O	m	e	Hf	Ac	I	Af	Ab
<i>Cyclotella stelligera</i> Cleve and Grunow 1882	x				x	x					x	x	
<i>Cyclotella meneghiniana</i> Kutzing, 1844	x				x			x				x	X
<i>Aulacoseira ambigua</i> (Grunow) Simonsen, 1979					x	x						x	
<i>Aulacoseira granulata</i> (Ehrenberg) Simonsen, 1979					x	x						x	
<i>Aulacoseira crenulata</i> (Ehrenberg) Thwaites, 1848													
<i>Aulacoseira granulata</i> var. <i>angustissima</i> (O. Muller) Simonsen, 1979					x	x						x	
<i>Aulacoseira distans</i> cf. <i>laevis</i> <i>Aulacoseira laevis</i> (Grunow) Krammer 1990	pH 6.8; alkalinity 185 meq l ⁻¹ (Haworth, personal communication, 2000)												
<i>Fragilaria construens</i> (Ehrenberg) Grunow, 1862	x	x			x	x						x	
<i>Fragilaria construens</i> variety ?	x	x			x	x						x	
<i>Fragilaria pinnata</i> Ehrenberg, 1843	x	x			x	x			x			x	
<i>Fragilaria brevistriata</i> Grunow in van Heurck, 1885	x				x	x						x	
<i>Brachysira vitrea</i> (Grunow) Ross in Halley, 1986	Low pH—diluted biotopes (Gasse, 1986)												
<i>Brachysira brebissonii</i> Ross in Hartley, 1986			x						x	x			(de Wolf, 1993)
<i>Cocconeis placentula</i> (Ehrenberg)	x	x				x			x		x	x	
<i>Cymbella silesiaca</i> Bleisch in Rabenhorst, 1864	x	x				x					x		
<i>Cymbella gracilis</i> (Ehrenberg 1843) Kutzing, 1844	Subaereal, cold-acidic waters (Gasse, 1986)												
<i>Cymbella microcephala</i> Grunow in Van Heurck, 1880	x		x			x					x	x	
<i>Cymbella aspera</i> (Ehrenberg) Peragallo, 1849	x	x		x		x						x	
<i>Epithemia turgida</i> (Ehrenberg) Kutzing, 1844	x	x							x			x	x
<i>Epithemia adnata</i> (Kutzing) 1838	x	x				x						x	x
<i>Stauroneis phoenicenteron</i> (Nitzsch) Ehrenberg, 1843	x					x					x		
<i>Eunotia serra</i> var. <i>serra</i> (Krammer & Lage Bertalot, 1991) Ehrenberg, 1834		x				x				x	x		(de Wolf, 1993)
<i>Eunotia bilunaris</i> var. <i>bilunaris</i> (Krammer & Lage Bertalot, 1991)	x			x		x				x	x		
<i>Eunotia formica</i> Ehrenberg, 1843		x				x					x		(de Wolf, 1993)
<i>Eunotia soleirolii</i> (Kutzing) Rabenhorst, 1864	x			x					x	x	x		
<i>Eunotia pectinalis</i> var. <i>undulata</i> (Ralfs) Rabenhorst, 1864	x			x		x				x			
<i>Eunotia flexuosa</i> (Brebisson) Kutzing, 1849	x			x		x				x			
<i>Gomphonema angustum</i> Agardh, 1834	x					x						x	
<i>Gomphonema gracile</i> Ehrenberg, 1838	x	x				x			x		x		
<i>Gomphonema truncatum</i> Ehrenberg, 1832	x					x					x	x	
<i>Nitzschia amphibia</i> Grunow (1862)	x				x	x		x				x	x
<i>Pinnularia gibba</i> Ehrenberg, 1841	x					x				x	x		
<i>Pinnularia hemiptera</i> (Kutzing, 1844)	Water with low mineral content (Germain, 1981)												
<i>Pinnularia bogotensis</i> (Grunow)*	Somewhat acidic ponds and with low mineral content (Patrick and Reimer 1966) (Gasse, 1986)												
<i>Pinnularia microstauron</i> (Ehrenberg) Cleve, 1881						x					x		
<i>Pinnularia maior</i> (Kutzing) Rabenhorst, 1853	x					x				x			
<i>Pinnularia stromatophora</i> (Grunow) Cleve, 1861			x						x	x			
<i>Pinnularia nobilis</i> Ehrenberg, 1843			x						x	x			(de Wolf, 1993)
<i>Sellaphora pupula</i> C. Mereschowsky 1902	x		x			x					x		
<i>Rhopalodia gibba</i> (Ehrenberg) O. Muller, 1895	x	x							x			x	x
<i>Tabellaria flocculosa</i> (Roth) Kutz	x				x				x	x			
<i>Navicula minuscula</i> var. <i>muralis</i> (Grunow) Lange-Bertalot	x		x	x		x			x	x	x		
<i>Navicula pseudoventralis</i> (Hustedt) 1953	x		x			x						x	
<i>Navicula schadei</i> Krasseke, 1929													
<i>Navicula radiosa</i> Kutzing, 1844	x		x			x					x		
<i>Achnanthes minutissima</i> var. <i>minutissima</i> Kutzing, 1833	x	x				x						x	
<i>Neidium iris</i> (Ehrenberg) Cleve, 1894	x		x								x		
<i>Synedra ulna</i> (Nitzsch) Ehrenberg	x	x			x	x						x	
<i>Synedra acus</i> Kutz	x	x			x	x						x	
<i>Neidium affine</i> (Ehrenberg) Pfitzer, 1871				x	x						x		
<i>Frustulina rhomboides</i> (Ehrenberg) De Toni, 1891*						x			x	x			(Gasse, 1986)

are found in Cretaceous marine outcrops in the area (Martínez, 1995). An increase in water turbulence and silica content are suggested by the dominance of the genus *Aulacoseira* (Kilham, 1971; Kilham *et al.*, 1986; Bradbury, 2000). Conductivity

oscillated between 140 $\mu\text{S cm}^{-1}$ and 310 $\mu\text{S cm}^{-1}$. These oscillations may correspond to instability of the lake-level, but they may also point to variations in salinity caused by the influence of ground water and/or river runoff into the lake. The

low concentration of magnetic minerals combined with high sedimentation rates is indicative of additional and/or different sources of sediments.

In zone FUQ-4 the increasing abundance of epiphytic and littoral diatom species (Fig. 2) suggests a gradual decrease in lake-level. Reconstructed pH values fluctuate between 7.6 and 7.8 (Figs 3 and 4). Conductivity—and salinity—were higher than in the zones below and correspond to a steady decrease in lake-level, pointing to a small volume of water with high salinity, i.e. a higher concentration of solutes. The pH values are higher than in the previous period, suggesting that the water input from local aquifers was lower. The presence of *Aulacoseira* spp. suggests an increase in water turbulence and in silica content (Van Landingham, 1964). The decline in both the magnetic mineral concentration and lake-level suggests a correlation between sediment input and lake size.

The absence of diatoms in zone FUQ-5 may be caused by valve dissolution owing to the peaty character of the sediment and/or to an exposure of the sediments to the atmosphere as a consequence of a drop in the lake-level. The absence of magnetic minerals suggests very low levels of erosion from the surrounding catchment. Because of the insufficient time control from this time on, we have not determined sedimentation rates.

The change in diatom composition at zone FUQ-6, compared with zone FUQ-4, can be interpreted as revealing low lake-level conditions. Littoral diatoms (*Fragilaria* spp.) are rare, there is an abundance of *A. distans* cf. *laevissima*, a diatom common in shallow lakes (E. Haworth, personal communication, 2000). As indicated above, pH and conductivity reconstructed from 'Calibrate' should be interpreted with caution owing the low percentage of matches (32%). In fact, the dominance of *A. distans* cf. *laevissima* rather suggests (i) low pH values in the order of 6.8 (in contrast to 8 indicated by 'Calibrate') and, (ii) lower conductivity than in the period of the zone FUQ-4 (Fig. 3). The dominance of *A. distans* cf. *laevissima* over *A. ambigua* may indicate a decrease of dissolved phosphorus in the water (Kilham *et al.*, 1986). Variations in P and pH may suggest a change in the trophic structure of the lake.

The dominance of *C. stelligera* in zone FUQ-7 suggests that the lake-level was relatively shallow, but deeper than at the end of the previous period. At about 690 yr BP (extrapolated) the peak in planktonic species indicates an increased water depth. The pH value was between 7.4 and 7.6. Conductivity decreased from $350 \mu\text{S cm}^{-1}$ during the earliest part of the period to $150 \mu\text{S cm}^{-1}$, and then stabilised at the latter value (Fig. 3). The $350 \mu\text{S cm}^{-1}$ value suggests an increased salinity. The reappearance of *A. ambigua* and the near disappearance of *A. distans* cf. *laevissima* may suggest an increase in phosphorous, turbulence or pH. As indicated before, DCA suggests that pH might be the main environmental variable determining the diatom distribution. Hence, it is probable that a return to alkaline conditions was the cause of the reappearance of *A. ambigua*. The reduced magnetic mineral concentration during this period suggests low sediment input.

Summary of the pollen-based reconstruction

The relevant part of the pollen record of core Fúquene-7, over the past ca. 24 000 ^{14}C yr, is summarised in Fig. 5. The following four pollen zones were recognised in the core interval from 700 to 280 cm. For more details see Mommersteeg (1998).

During pollen zone Y (780–535 cm; period of 24 035 to 13 925 ^{14}C yr BP) the regional vegetation is dominated by grassparamo. In the last phase of this period Andean forest increased slightly. *Hydrocotyle* was a common element in the margins of the lake, indicative of a low lake-level. Pollen from this interval suggests low lake-levels and extensive dry vegetation.

During pollen zone Z1 (535–415 cm; period of 13 925 to 7225 ^{14}C yr BP, including a hiatus) the regional vegetation was composed of humid *Quercus*-dominated forest. This indicates that wet conditions must have prevailed; however, in the middle of this period the oak forest was partly replaced by grassy vegetation, i.e. the upper forest line moved down slope. This is indicative of a temporary return to drier and cooler conditions that could explain the hiatus corresponding to the interval between 13 110–7780 ^{14}C yr BP.

During pollen zone Z2 (415–325 cm; period of 7225 to 5540 ^{14}C yr BP) *Quercus*-dominated forest continued to be the most abundant around the lake. The increase of *Potamogeton* was probably related to higher temperatures.

During pollen zone Z3 (325–280 cm; period of 5540 ^{14}C yr BP to recent) the lake, as well as its surroundings, were subject to human impact. For this reason Mommersteeg (1998) did not analyse this period. However, the pollen diagram (Fig. 5) shows an increase in subparamo, marsh and aquatic elements, and a decrease in *Quercus* and *Alnus*.

Environmental reconstruction based on a multiproxy approach

In this section we present the history of environmental and climatic changes in Lake Fúquene and its surroundings. The reconstruction of the lake history is based on evidence from diatoms, pollen records of lake shore and aquatic taxa, radiocarbon dating and sediment analysis. The development of the lake is placed in the regional context on the basis of regional information from the pollen record. Figure 6 shows the different periods that resulted from superimposing the diatom and the pollen zonation and the comparison with the climatic periods of Van 't Veer *et al.* (2000). From both proxies nine discrete periods can be recognised.

From 19 700 to 14 200 ^{14}C yr BP (period 1): all proxies showed stable dry and cold glacial conditions. The lake was low and chemically stable; it was probably a closed hydrological system. Paramo and grassparamo vegetation surrounded the lake and the temperature was about 4 to 6 °C lower than today (Mommersteeg, 1998; Van 't Veer *et al.*, 2000). Although data from the same period are scarce in Colombia, Wille *et al.* (2000) recorded dry and cold conditions in the southern part of the Western Cordillera of Colombia. This period is correlated with pollen zone W (ca. 22 000–14 200 ^{14}C yr BP) from Van 't Veer *et al.* (2000), zone Y from Mommersteeg (1998), zone W5 from Van Geel and Van der Hammen (1973), and diatom zone FUQ-1.

From ca. 14 200 to ca. 13 925–13 110 ^{14}C yr BP (period 2): this period records transitional conditions from a dry cold glacial to a warmer and a more humid Late-glacial. The lake-level started to increase and probably the water became more dilute as a consequence of increasing volume. It was a period of changes in land cover, presence of open rocky soil, and erosion as reflected in the increase in the coarser sediments and in *Dodonaea* (Van 't Veer *et al.*, 2000); eventually, however, a *Quercus*-dominated forest became established in the area. This interval includes the transition from pollen zone Y to Z1

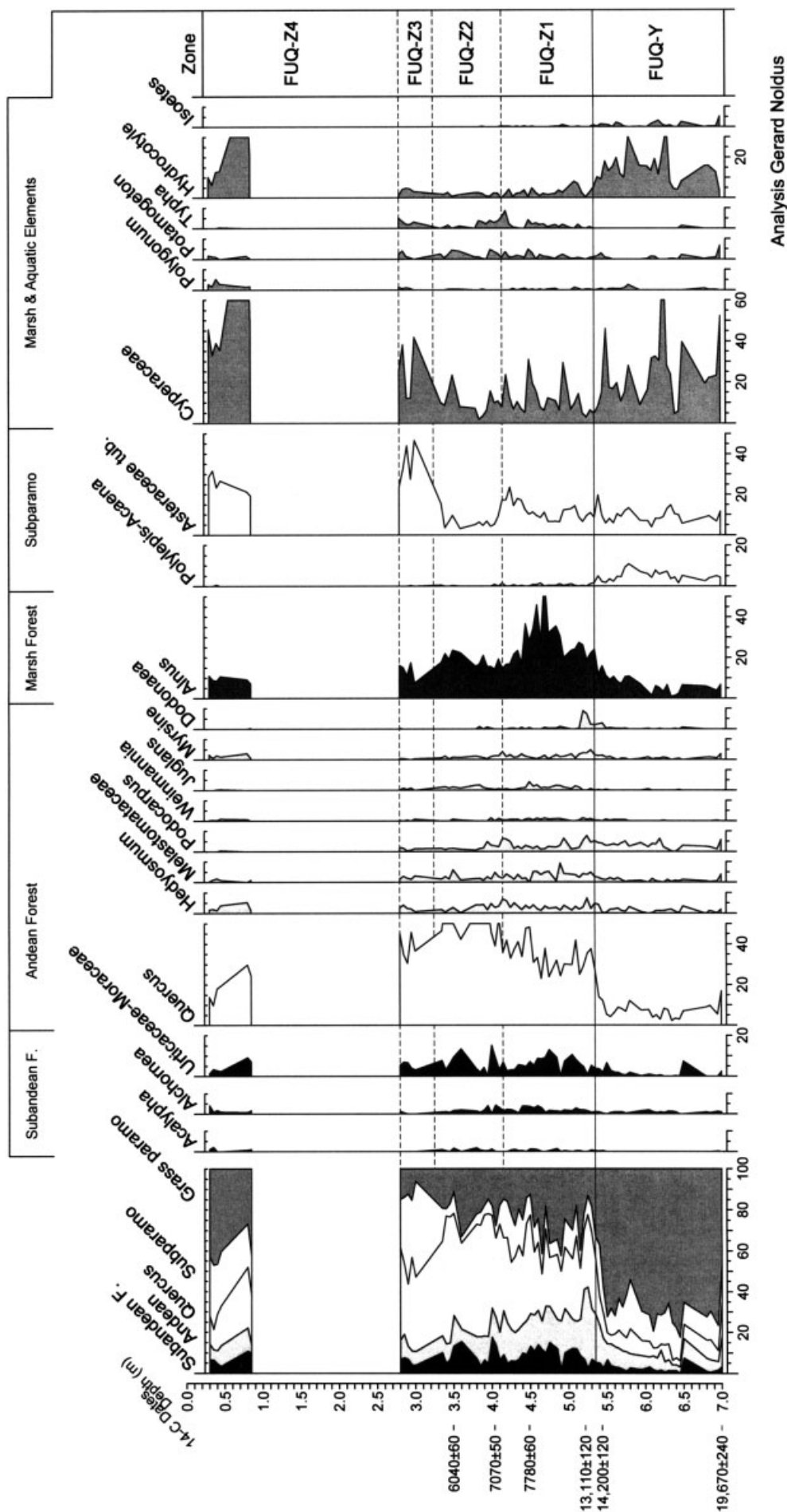


Figure 5 Pollen percentage diagram of the upper 7 m of core Fúquene-7 showing selected taxa that are most relevant for the present comparison of the diatom-based and pollen-based lake-level histories. Adapted after Mommersteeg (1998)

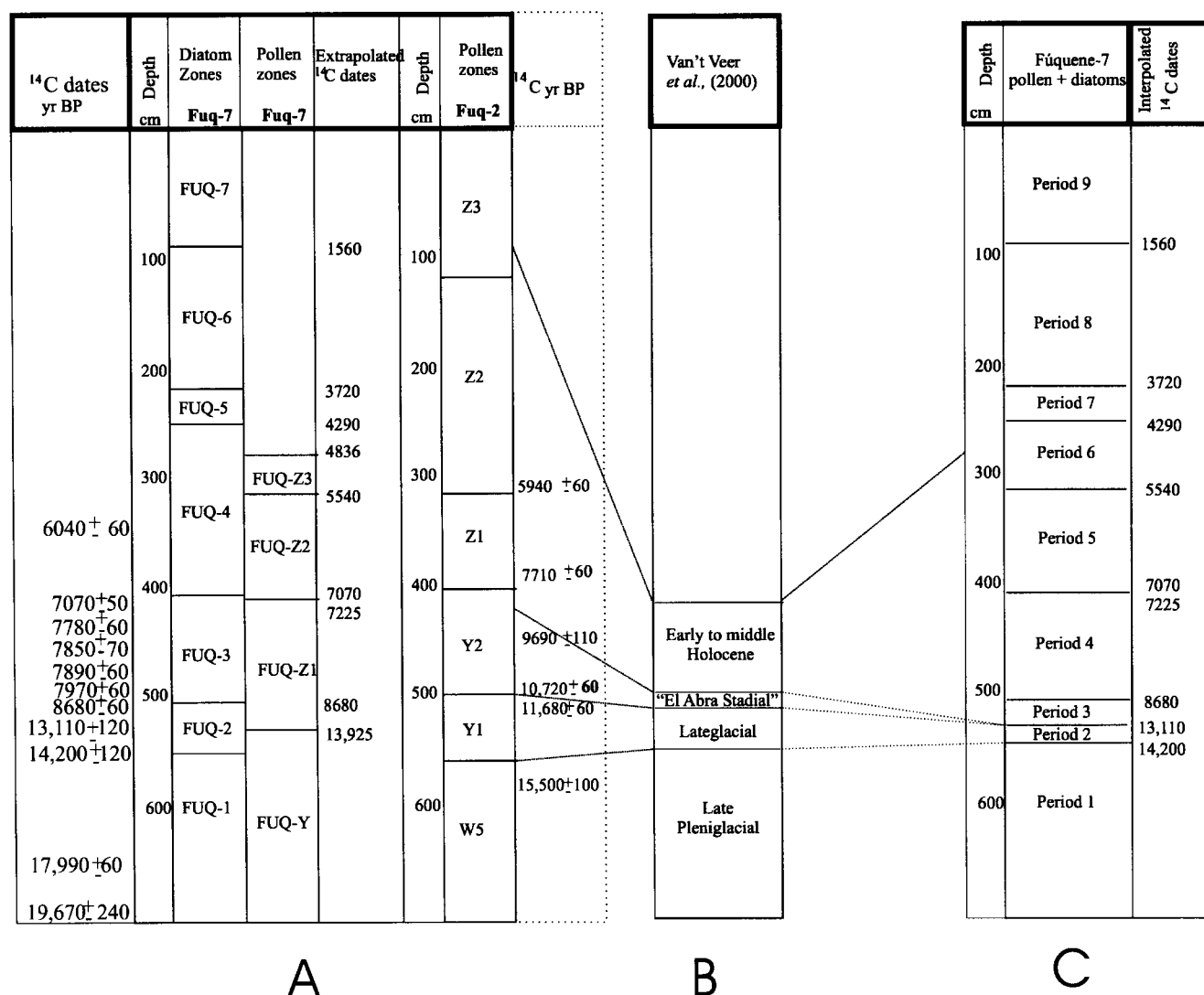


Figure 6 Synthesis of diatom-based and pollen-based records of environmental change and its zonation based on cores Fúquene-7 and Fúquene-2. From left to right: column A compares pollen-based and diatom-based zones from core Fúquene 7 and Fúquene-2 (Van Geel and Van der Hammen, 1973; Mommersteeg, 1998). In column B we present the climatic periods recognised by Van't Veer *et al.* (2000), and column C shows the different environmental periods that result from the overlap of diatom and pollen zones

from Mommersteeg (1998), Y1 pollen zone from Van 't Veer *et al.* (2000), and FUQ-2 diatom zone. This period of increased temperatures and humid conditions is known in Colombia as the Guantiva Interstadial (Van Geel and Van der Hammen, 1973; Mommersteeg, 1998; Van 't Veer *et al.*, 2000).

From 13 110 to 8680 ¹⁴C yr BP (period 3): there are no records for the period from 13 110 to 8680 ¹⁴C yr BP owing to a gap in the sedimentary record. The stratigraphy of the core shows a sharp contact between underlying dark fine sediments and light and coarser sediments. According to Van 't Veer *et al.* (2000) and Mommersteeg (1998) this hiatus occurred at the transition from the Guantiva Interstadial to the El Abra Stadial and covers the full El Abra Stadial. The El Abra Stadial, which corresponds to the Younger Dryas event, features a decrease in effective precipitation (Van 't Veer *et al.*, 2000). During this event the Andes of Colombia had a cold and dry climate (Van 't Veer *et al.*, 2000), hence, the sedimentary gap in Fúquene-7 reflects a drop in lake-level to somewhere below the coring site. In the Cauca Valley, in the southwest of Colombia, Berrío *et al.* (2002a) report dry and warm climates at ca. 10 500 ¹⁴C yr BP. In the Llanos Orientales, Behling and Hooghiemstra (1998) record a drop in temperature from 10 700 to 10 000 ¹⁴C yr BP. The Younger Dryas (11 000–10 000 ¹⁴C yr BP) in the

north of South America was, in general terms, cold and dry, as reported by Muhs and Zárate (2001) for eastern Colombia and Venezuela, by Marchant *et al.* (2002) for a synthesis of Colombian sites, by Fritz *et al.* (2001) for the Caribbean and Lake Valencia (Venezuela), and by Haug *et al.* (2001) for the Cariaco Basin (northern shelf of Venezuela). This period also includes the transition from the dry and cold El Abra Stadial (Younger Dryas) to a widely recognised warm and wet early Holocene (Martin *et al.*, 1997; Haug *et al.*, 2001). This period corresponds to the diatom zone FUQ-2.

From 8680 to 7070 ¹⁴C yr BP (period 4): all proxies indicate warm and humid climatic conditions. During this period the lake reached the highest level recorded since 19 700 ¹⁴C yr BP, with a stable water chemistry. The surroundings were colonised by humid *Quercus* dominated forest and the upper forest line was between 3200 and 3300 m. Martin *et al.* (1997) and Haug *et al.* (2001) suggest that the abundant precipitation recorded in the north of South America was the result of a more northerly position of the ITCZ. This period is included in the Z2 pollen zone of Van 't Veer *et al.* (2000), zones Z1 and Z2 from Mommersteeg (1998) and diatom zone FUQ-3. A temporary drier phase occurred at ca. 7780 ¹⁴C yr BP, causing a drop in lake-level. This drier period was also recorded in sediments

from the southwest of Colombia, where maximum dryness was reached by 7500 ^{14}C yr BP (Berrío *et al.*, 2002a). Other records from the eastern savannas of the Llanos Orientales indicate similar conditions (Behling and Hooghiemstra, 1998; Behling and Hooghiemstra, 2000; Berrío *et al.*, 2002b).

From 7070 to ca. 5500 ^{14}C yr BP (period 5): decreasing lake-levels, unstable sedimentation and water chemistry, increased presence of rocky soil (*Dodonaea*) and greater abundance of *Urticaceae* point to a period of instability and the onset of drier climates. Dry conditions were already present at this time in the savannas of the Llanos Orientales and in the Cauca Valley in the southwest of Colombia (Berrío *et al.*, 2002a,b). Haugh *et al.* (2001) attribute the change to a drier climate in the Holocene as a consequence of the southward shift of the ITCZ. This shift, prevailing today, causes drier climates in the Cariaco basin (north Venezuela) and brings more precipitation to the Amazon region. This period is correlated with Z2 pollen zone from Van 't Veer *et al.* (2000) and Mommersteeg (1998), and diatom zone FUQ-4.

From ca. 5500 to 4300 ^{14}C yr BP (period 6): lower lake-levels and drier climates prevailed during this period. The Andean forest moved downslope again and elements from the subparamo were frequent in the basin. Van Geel and Van der Hammen (1973) suggested that the increase in dryness was first felt in the southern part of the lake and eventually in the north. Van Geel and Van der Hammen (1973) and Mommersteeg (1998) suggested land occupation by humans caused forest destruction and soil erosion. This period is correlated with pollen zone Z3 (Mommersteeg, 1998) and Z2 (Van Geel and Van der Hammen, 1973), and diatom zone FUQ-4.

From ca. 4300 to ca. 3700 ^{14}C yr BP (period 7): during this period there is a change in the stratigraphy of the core from detrital material to a peat. The absence of diatoms and the peaty sediments suggest a lowered lake-level and occasional desiccation. This period corresponds to the Z2 pollen zone from Fúquene-2.

From ca. 3700 to ca. 1600 ^{14}C yr BP (period 8): during this period drier and cooler conditions were established in the basin. The lake-level was relatively low and water became more acidified and nutrient rich. The increase in erosion in the catchment is indicated by all proxies, confirming human influence. This period is correlated with diatom zone FUQ-6 and pollen zones Z2–Z3 from Fúquene-2.

From ca. 1600 ^{14}C yr BP to present (period 9): climatic conditions similar to the previous period were maintained. Some changes in hydrochemistry and in lake-level are indicated by diatoms and sediments, however, it is difficult to know whether they were caused by human influence or by changes in climate. This period corresponds to diatom zone FUQ-7 and pollen zone Z3 from Fúquene-2.

Conclusions

We conclude that diatom and pollen assemblages recorded synchronously most of the environmental changes than occurred in the basin since ca. 19 700 ^{14}C yr BP. The onset of drier conditions during the middle Holocene (ca. 7070 ^{14}C yr BP), however, appear earlier in the diatom and sedimentary record than in the pollen record.

The climate patterns from the Late-glacial and the Holocene in our new record from Lake Fúquene are similar to other records from Panama, Venezuela and the Caribbean (Fritz *et al.*, 2001; Bradbury *et al.*, 2001; Haugh *et al.*, 2001). Relatively dry climates predominated during glacial times.

A marked dry and cold El Abra Stadial (equivalent to the Younger Dryas in Europe) was registered in Fúquene-7 by a hiatus occurring sometime between about 13 000 and 8700 ^{14}C yr BP and recorded in Laguna Los Lirios between 11 300 and 9800 ^{14}C yr BP (Bradbury *et al.*, 2001), in Lake Valencia from ca. 10 000 to ca. 9000 ^{14}C yr BP (Fritz *et al.*, 2001), and in the Cariaco basin (Haugh *et al.*, 2001) from ca. 12 600 to 11 500 cal. yr BP (corresponding to 10 500 to ca. 10 000 ^{14}C yr BP). During the early Holocene, characterised by humid and warm climates, the lake reached its maximum extension. This increase in precipitation in the north of South America was the consequence of a northern position of the ITCZ during this period (Martin *et al.*, 1997; Haugh *et al.*, 2001). The onset of drier climates occurred in Fúquene at ca. 7070 ^{14}C yr BP and prevail until today. These middle Holocene drier climates are registered in other places in the savannas of the Llanos Orientales and the Cauca Valley in Colombia (Berrío *et al.*, 2002a,b). Marchant *et al.* (2001, 2002) show a general change in the vegetation of Colombia as a consequence of drier climatic conditions between 6500 and 5000 ^{14}C yr BP. In Panama (Lake La Yeguada) limnological records suggest a dry phase between 7000 and 3800 ^{14}C yr BP (Fritz *et al.*, 2001) and in Venezuela (Lake Valencia) a drier phase was recorded between 7000 and 6000 ^{14}C yr BP (Fritz *et al.*, 2001). According to Haugh *et al.* (2001) this drier climate phase results from the southward shift of the ITCZ to its current average position. We conclude that the environmental and lake-level changes recorded in this core are driven by changes in precipitation owing to shifts of the ITCZ.

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