



Holocene paleolimnological reconstruction of a high altitude Colombian tropical lake



A.Y.V. Cardozo^{a,b,*}, Doriedson Ferrreira Gomes^a, Eduardo Mendes da Silva^a, S.R.E. Duque^c, J.O.Ch. Rangel^d, Abdelfettah Sifeddine^{e,f}, Bruno Turcq^g, Ana Luiza Spadano Albuquerque^e

^a Instituto de Biologia, Departamento de Botânica, Universidade Federal da Bahia, Rua Barão de Jeremoabo 147, CEP: 40170115 Salvador, Bahia, Brazil

^b Unidad de Ecología en Sistemas Acuáticos, Escuela de Ciencias Biológicas, Universidad Pedagógica y Tecnológica de Colombia, Avenida Central del Norte, Tunja, Boyacá, Colombia

^c Instituto Amazónico de Investigaciones Imani, Universidad Nacional, Km 2 via Tarapacá, Leticia, Amazonas, Colombia

^d Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Ciudad Universitaria, Cra 30 #45-03, Bogotá, Cundinamarca, Colombia

^e Instituto de Química, Departamento de Geoquímica Ambiental, Universidade Federal Fluminense, Rua Outeiro de São João Baptista, CEP: 24020015 Niterói, Rio de Janeiro, Brazil

^f Institut de Recherche pour le Développement, France

^g IRD LOCEAN (UPMC, CNRS, IRD, MNHN), 32 av Henri Varagnat, 93143 Bondy Cedex, France

ARTICLE INFO

Article history:

Received 12 June 2013

Received in revised form 16 February 2014

Accepted 6 March 2014

Available online 15 March 2014

Keywords:

Paleohydrology

Late Holocene

Diatoms

Sedimentary

Organic geochemistry

Lake Tota

ABSTRACT

Aquatic environments in the high-Andean may be quite vulnerable to climatic conditions and hydrological processes (precipitation/evaporation) that have the potential to alter water levels and chemistry. This study reconstructs the paleohydrological history of Lake Tota, Colombia, to provide a record of environmental changes in the eastern flank of the Colombian Andes during the late Holocene. A 54 cm core was collected at the margin of the lake at a depth of 1.5 m, and the paleohydrological reconstructions were based on changes in diatom assemblages, granulometry, and bulk organic geochemical parameters. The core was subdivided into 5 biozones by assessing the significance of the variance among the CONISS clusters. Biozone T5 (base, 4000 calibrated years BP) was dominated by the planktonic diatom *Discostella stelligera* and was deposited in a period of high-water level. Sedimentation during this period was rich in carbon due to phytoplanktonic production; the granulometry data suggests that the lake was under high to moderate hydrological dynamic conditions, indicating active deposition at the river delta front. Biozone T4, beginning at 3600 cal. yrs BP, was dominated by three species *D. stelligera*, *Cocconeis placentula* var. *lineata* and *Fragilaria sensu lato*, and this association could indicate that the lake was under the influence of large fluctuations in water level. This interpretation is supported by granulometry and geochemical data, particularly by the low levels of total organic carbon (TOC). In biozone T3, corresponding to 3000 cal. yrs BP, we found a lowering of the water level, suggested by low levels of TOC. Poor granulometric sorting and higher carbon/nitrogen (C/N) ratios suggest a macrophyte influence on the sedimentation, avoiding direct deltaic influence. In this biozone the benthic diatom *F. sensu lato* group was dominant. In biozone T2, starting 2400 cal. yrs BP, the proxies indicate that the lake experienced increasing water levels and that stronger circulation patterns occurred in the water column than in the preceding periods, as inferred by the presence of *Aulacoseira granulata* a ticolanktonic species. The sediment in this biozone is well sorted and finer, indicating a greater depth. Biozone T1 at the top of the core and since 2000 cal. yrs BP to the present, evidence for a recent reduction in water level of Lake Tota can be deduced by the presence of *Achnanthisidium minutissimum* var. *minutissimum*.

© 2014 Elsevier B.V. All rights reserved.

1. Introduction

The greatest variety of aquatic environments (including small to large lakes) is found in the high-Andean zone above 3000 m (Izurieta, 2007; Maldonado et al., 2011). These environments can be especially vulnerable to direct climatic effects by virtue of changes to their hydrological processes (Marengo et al., 2011). As such, these ecosystems can be used as Holocene climatic sensors. The main factors that influence the climate in this zone are the presence of the moisture of the Amazon

* Corresponding author at: Instituto de Biologia, Departamento de Botânica, Universidade Federal da Bahia, Rua Barão de Jeremoabo 147, CEP: 40170115 Salvador, Bahia, Brazil. Phone: +55 71 32836532 32836531.

E-mail addresses: yohanacardozo@yahoo.es (A.Y.V. Cardozo), dfgomes@ufba.br (D.F. Gomes), marenba@gmail.com (E.M. da Silva), srduque@unal.edu.co (S.R.E. Duque), jorangelc@unal.edu.co (J.O.C. Rangel), abdel.sifeddine@ird.fr (A. Sifeddine), bruno.turcq@ird.fr (B. Turcq), analuiza@geoq.uff.br (A.L.S. Albuquerque).

forest to the east, the displacement of the Inter-Tropical Convergence Zone (ITCZ), and the presence of the Trade Winds to the north. At high elevations, the subtropical jet stream and the permanent high-pressure system of the South Pacific and South Atlantic are important drivers of climatic changes (Martínez et al., 2011).

Water levels and chemistry in the lake water balance may be used as markers for local and regional hydrology (Smol, 2002; Birks and Birks, 2006; Wolin and Stone, 2010). Because lakes are inextricably linked to the local climatic systems, their water level and chemistry are manifestations of the balance between inputs (i.e., precipitation, runoff, and groundwater flow) and outputs (i.e., evaporation, flow releases, and groundwater recharge) (Mason et al., 1994). Thus, changes in water balance (precipitation/evaporation) caused by climatic changes or human activities have the potential to modify lake water levels and chemistry (e.g., pH and salinity) that may affect the specific composition of diatoms. Given this, diatoms may be good indicators of past hydrological processes.

Paleolimnological techniques may be used to investigate the modes and rates of change, offering a historically unique opportunity to evaluate the response of lakes to environmental changes, including those resulting from human activities (Smol, 2002). Environmental changes may affect most aspects of the functioning of lakes (Battarbee, 2000; Lotter and Birks, 2003) and, as such, understanding these changes may be of great relevance to gain predictive insights to future human-induced lake developments.

Paleolimnological studies in Colombia have traditionally been based on the analysis of Quaternary pollen profiles in the highland savanna of Bogotá, Western Cordillera, Llanos Orientales (eastern lowland savannas) and in the Amazon (Behling and Hooghiemstra, 1998, 1999, 2000; Van der Hammen and Hooghiemstra, 2000; Van't Veer et al., 2000; Marchant et al., 2001a; Wille et al., 2003; Velásquez and Hooghiemstra, 2013). In recent investigations, however, diatoms have been used for paleolimnological studies (Vélez et al., 2001, 2003, 2005a, 2005b, 2006).

The Colombian paleoclimate studies show that in the Andes (Laguna Fúquene), climatic conditions were dry during the middle Holocene (Van't Veer et al., 2000). The records of the Llanos Orientales of Colombia (Lagunas Las Margaritas, Loma Linda, Sardinas, Angel, Carimagua and Chenevo) show that between 5800 and 3800 ¹⁴C years BP, these lakes changed to savanna gallery forests and were associated

with short dry periods followed by longer duration of increased rainfall (Behling and Hooghiemstra, 1998, 1999, 2000). These more humid conditions were also recorded in the reconstruction of Colombian biomes, inferred from changes between 4000 and 3000 ¹⁴C years BP (Marchant et al., 2001b).

In order to improve our understanding of climate and environmental changes during the Holocene in Colombia, we surveyed the fossil diatom assemblages, granulometry and bulk organic geochemical parameters preserved in the sediments of Lake Tota in the Colombian Cordillera Oriental. For this high altitude lake, we assessed the paleohydrological changes (P/E balance) that occurred during the middle and late Holocene.

2. Study area

Lake Tota is the largest mountain lake in the Colombian Andes, located at 3015 m above sea level at 5° 33' 40"N and 72° 53' 52"W (between the towns of Aquitania, Tota and Cúitiva; Fig. 1). It is located in the province of High Mountain in the Colombian Cordillera Oriental, in the southeast part of the state of Boyacá (Monroy, 2003; Aranguren-Riaño et al., 2011). The lake is a natural reservoir of tectonic-glacial origin, with an area of 60 km² and an average depth of 30 m. According to González et al. (2008), Lake Tota is a well-oxygenated, warm polymictic system, neutral in pH, with few minerals, and categorized as oligo-mesotrophic (Table 1). The entire basin encompasses a total area of 201 km² and its natural outflow gives origin to the Upía River, a tributary of the Orinoco River. The lake is also the main source for irrigation within the basin and supplies the urban and industrial needs of more than 200,000 people in ten municipalities (Cañón and Valdes, 2011).

Although monthly precipitation curves are bimodal in the interandean region (González et al., 2008), rainfall and evaporation series are mostly monomodal in the Tota Lake basin, with higher precipitation (lower evaporation rates) occurring between June and August (Cañón and Valdes, 2011). Precipitation begins in April, when the South American Monsoon relaxes, the insolation is at a maximum at the equator (equinox), and the convection in Amazonia is centered at 0°, 70°W. The precipitation maximum occurs in June when the ITCZ is located between 5 and 10°N on both the Atlantic and Pacific Oceans (Poveda et al., 2006). Then the Trade Wind circulation is at its maximum, bringing wetness

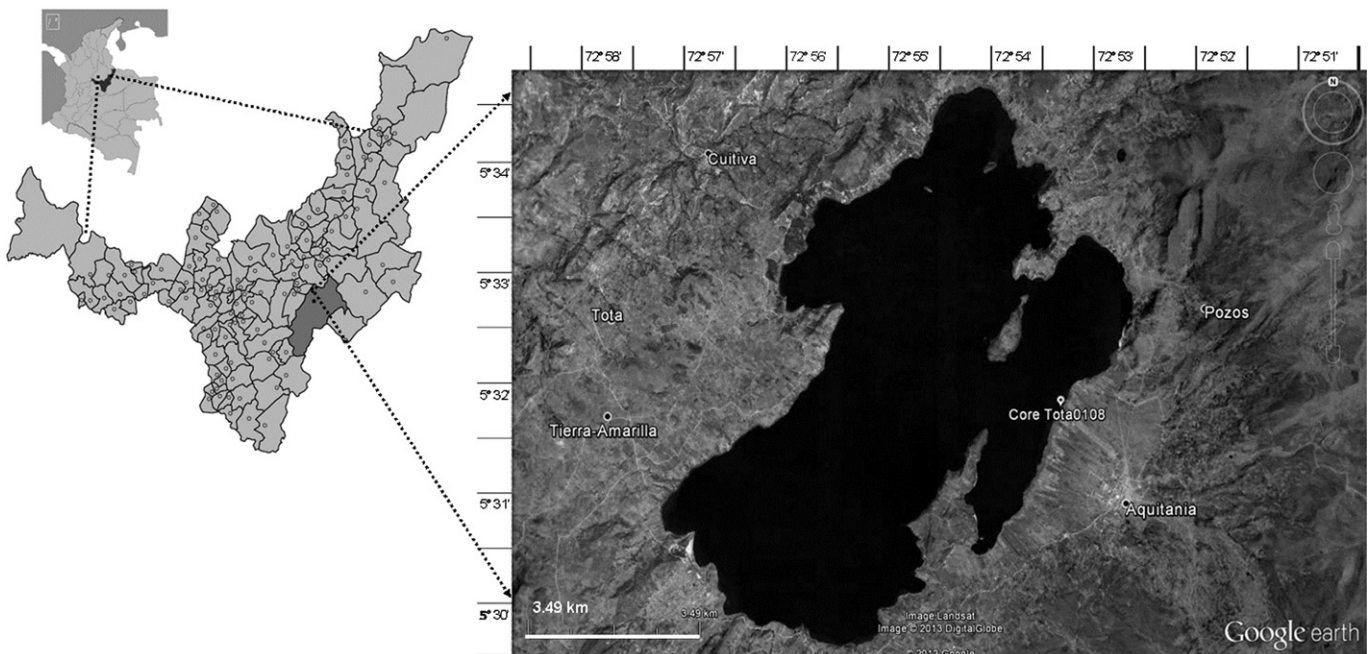


Fig. 1. Location of the study area showing the core sampling. http://commons.wikimedia.org/wiki/File:3AMunsBoyaca_Aquitania.png.

Table 1
Morphometric, meteorological, hydrological and limnological data of Lake Tota.

Morphometric data	Values
Basin area	201 km ²
Lake area	60 km ²
Maximum length (northeast)	12 km
Maximum width	6.5 km
Perimeter	47 km
Volume (elevation 3015)	1942.5 × 10 ⁶ m ³
Average depth (Lake Chico)	30 m
Maximum depth (Great Lake)	61 m
Minimum recorded (1998)	3013.62 m
Highest level recorded (1971)	3015.70 m
Fluctuation record high	1.86 m
Corresponding volume of water loss	120 × 10 ⁶ m ³
Decline in the level of the lake	1.8 cm yr ⁻¹
Water renewal time	29.8 yrs
Sedimentation rate	2.27 × 10 ⁶ m ³ yr ⁻¹
Rate of sediment yield estimated SG = 1.8	4.08 × 10 ⁶ ton yr ⁻¹

From Hidroestudios Ltda (1978), Cañón (2001), Monroy (2003), Cardozo and Pita (2004) and Gonzalez et al. (2008).

from Amazonia and the Atlantic Ocean (Sakamoto et al., 2011). This mechanism is perturbed by El Niño events that reduce precipitation in northern Amazonia and dislocate convective activities to the South and West (Poveda et al., 2006). During El Niño events, a decrease in the Lake Tota level was observed (Cañón and Valdes, 2011). According to these authors, ENSO and PDO are the main cause of interannual variability of the lake level.

3. Materials and methods

3.1. Field work and sample processing

The Tota0108 core was collected at a water depth of 1.5 m by scuba diving using a hand-operated acrylic core sampler. This core (54 cm in length and 11 cm in diameter) was taken from the littoral zone next to delta of the Toba River and within a bank of *Egeria densa* Planchon (Hydrocharitaceae) in the northeast basin of the lake, called Sector Lake Chico (5° 32′ 01.1″ N and 72° 53′ 43.9″ W) (Fig. 1). Once the sediment core was retrieved, we proceeded with the lithostratigraphical description (texture and color) based on the Munsell color chart. The core was subsampled at intervals of 0.5 cm. These samples were packed in labeled plastic bags and stored at 4 °C.

3.2. Chronology

Seven bulk samples were collected at depths ranging from 7 to 8 cm, 17 to 18 cm, 20 to 21 cm, 31 to 32 cm, 40 to 41 cm, 47 to 48 cm and 52 to 53 cm for ¹⁴C accelerator mass spectroscopy (AMS) dating. Radiocarbon dating was done at the Laboratoire de Mesures Carbone 14, France and the NSF-Arizona AMS Laboratory, U.S.A. (Table 2). These radiocarbon ages were transformed to calibrated years BP using the South Hemisphere curve (SHCal04) (McCormac et al., 2004) available in the program

Table 2
AMS ¹⁴C radiocarbon ages and calibrated ages of selected samples from Core Tota0108.

Laboratory code	Depth (cm)	Nature	Radiocarbon age ¹⁴ C yr BP	δ ¹³ C	95.4% (2σ) cal. age ranges (BP) ^a	Relative area under distribution	Average of age range (cal. yr BP)	Cumulated mass (g cm ³ yr ⁻¹)
AA90174	7–8	Sediment	1868 ± 34	−22.9	1687–1829	0.865	1758	0.010
AA90175	17–18 ^b	Sediment	4317 ± 37	−25.7				
SacA19127	20–21 ^b	Sediment	5010 ± 35	−26.3				
SacA19128	31–32 ^b	Sediment	3857 ± 37	−25.1				
AA90177	40–41	Sediment	3435 ± 30	−26.4	3552–3704	0.928	3628	0.150
AA90178	47–48	Sediment	3511 ± 38	−24.5	3613–3839	0.995	3726	0.057
SacA19129	52–53	Sediment	3685 ± 35	−25.8	3838–4010	0.850	3924	0.029

^a Age calibration was performed with the SHCal04 ¹⁴C, using calibration data from McCormac et al. (2004).

^b Samples marked by an asterisk were rejected (see text): no calibrated ages are given.

CALIB 5.0.2 (Stuiver et al., 2005) (Table 2). We used a second-term polynomial curve to construct an age-depth model for the core (Fig. 2).

3.3. Granulometry

To determine the grain size for each sample from the Tota0108 core, approximately 3.0 g of wet sediment was placed in a beaker and first treated with 30 ml of hydrogen peroxide (30 vol) and potassium dichromate for organic matter removal and then treated with 10 ml HCl (10%) to remove carbonates (Battarbee et al., 2001; Allen and Thornley, 2004). These treatments were conducted on hotplates adjusted to maintain the solution at 70 °C. After each of these treatments, the samples were centrifuged at 3500 rpm for 8 min and then the liquid phase was discarded (Vaasma, 2008). Samples were then washed with distilled water until neutrality. To avoid grain flocculation during pre-treatment, a 1% solution of sodium hexametaphosphate Na(PO₃)₆ (Calgon) was used followed by 24 h of agitation on a mechanical vibrator (Andreola et al., 2004; Gray et al., 2010). Grain-size distributions were measured with a laser particle analyzer CILAS (Mod.1064), with detection range between 0.02 μm and 2000 μm.

3.4. Isotopic and elementary composition

Total organic carbon (TOC), total nitrogen (TN), and δ¹³C and δ¹⁵N isotopes were determined at California University (UC Davis Stable Isotope Facility), USA, using a PDZ Europa ANCA-GSL elemental analyzer interfaced with a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd. Cheshire, UK).

3.5. Biological analysis

For the extraction of the diatom valves, standard techniques (Battarbee, 1986; Battarbee et al., 2001) were applied. Approximately 1.0 g of wet sediment was placed in a beaker for oxidation by hydrogen peroxide (30 vol), which was continually added to the sample until frothing ceased so as to remove all organic matter. The samples were heated at 80 °C to increase the speed and completeness of hydrogen peroxide digestion. Finally, samples were rinsed with distilled water. This procedure was repeated until the samples reached neutral pH. Permanent slides were prepared by putting 1 ml of each treated sample on a coverslip. The coverslips were air-dried and mounted with Naphrax (IR 1.74) onto glass microscope slides.

Diatom identification was performed following Hustedt (1961–1969), Patrick and Reimer (1966), Metzeltin and Lange-Bertalot (1998), and Metzeltin et al. (2005). The nomenclatural taxonomic criterion followed Round et al. (1990). Slides were observed using an Olympus CX40 microscope at 1000× magnification. After identification, the valves and their identifiable fragments were counted along transects perpendicular to the main slide axis. A minimum of 400 valves were counted, considering as identifiable fragment of centric diatoms those that showed the central part of the valve, in araphid pennates those that showed more than half of

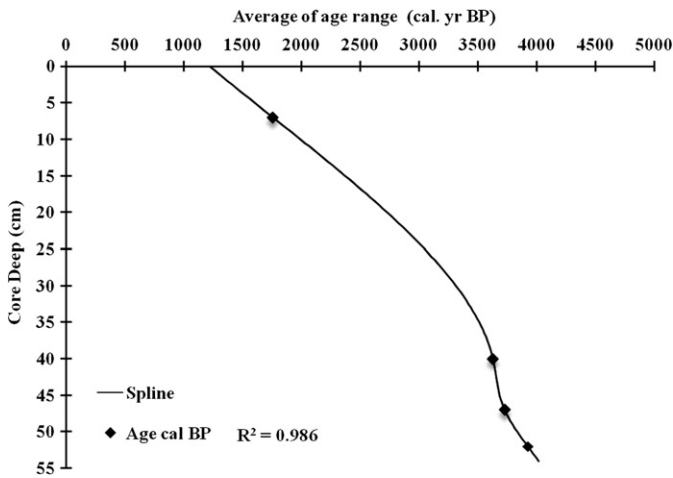


Fig. 2. AMS ^{14}C radiocarbon ages vs. depth of core Tota0108.

the valve, and in pennates those that showed the raphe system and the central area (Battarbee et al., 2001).

3.6. Statistical analysis

Assemblages of diatom counts of the core were converted to relative frequency (McCune et al., 2002) and drawn in stratigraphic profile generated in the computer program C2, vs.1.5 (Juggins, 2007). To generate the zonation of the core for diatom data, cluster analysis CONISS (Grimm, 1987) using dissimilarity matrix of squared Euclidian distances was conducted. The broken stick test was applied to assess the significance of the variance among the clusters (zonation) using the sum-of-total squares (Bennett, 1996), available in the application Rioja (version 0.5–6, Juggins, 2009). Only taxa that were present with a relative abundance of >1% in at least one sample were included in the analysis (Abbott et al., 2000). Prior to analysis, the relative abundance diatom data was square-root transformed to stabilize the variance (Hassan et al., 2009). Analyses were conducted using R v.2.13.1 (R Development Core Team, 2009).

Detrended Correspondence Analysis (DCA) was performed to determine Hill's N_2 , a measure of diversity equivalent to the inverse of the Simpson's diversity measure and to determine the gradient length (Hill and Gauch, 1980; Birks, 1998). The size of the gradient is particularly useful to determine the more appropriate technique (i.e., unimodal or linear) to analyze the data (as in Lepš and Šmilauer, 2003). After defining the size of the gradient (DCA axis-1 gradient was less than 2 standard deviation units, indicating a linear response), a Principal Component Analysis (PCA) was run in order to complement the results obtained by CONISS.

4. Results

4.1. Stratigraphy and chronology of the core

The chronological data in ^{14}C year and cal. yr BP for the Tota0108 core are summarized in Table 2. Three of the seven dates appear anomalous. The depositional ages of 4317 ± 37 cal. yrs BP at 17 cm, 5010 ± 35 cal. yrs BP at 20 cm, and 3857 ± 36 cal. yr BP at 31 cm are considered outliers and are not used to construct the depth-age scale in Fig. 2. The core samples from the 17 cm and 31 cm levels are composed of sand and very coarse silt whereas at the 20 cm level, the sample is composed of silty clay and medium coarse silt with wood fragments. These sediments were probably deposited under turbulent conditions, making dating of these three sections unreliable. After rejection of these three anomalous dates, the base of the core corresponds to about 4000 cal. yr BP (Fig. 2).

4.2. Description of the fossil diatom, sedimentary and geochemical stratigraphy from Core Tota0108

A total of 94 diatom taxa were identified, representing 40 genera and 24 families, in the 108 samples of Core Tota0108 that were analyzed. The diatom taxa occurring with a relative abundance of at least 1% in at least three samples constitute the dataset (i.e., a total of 61 taxa) from which statistical analyses were conducted. In Table 3 the interpretation of ecological conditions such as habitat, pH and nutrient status based on the modern ecology for only the diatom species that accounted for 95% (28 taxa) of the total relative abundance in Core Tota0108 is shown.

For simplicity of graphical representation, the data were summarized in major genera (i.e., *Fragilaria sensu lato* consisted of *Pseudostaurosira brevistriata* (Grunow) var. *brevistriata*, *Pseudostaurosira brevisstrata* var. *inflata* (Pantocsek) Hartley, *Staurosira venter* (Ehrenberg) Kobayasi, *Staurosirella pinnata* (Ehrenberg) Williams and Round and *Staurosirella leptostauron* var. *dubia* (Grunow) Edlund), and the most common species were shown in Fig. 3. After combining the results from PCA and CONISS cluster analyses, in which the significance of the variance among these clusters was assessed, the core was divided into five main biozones (Fig. 3).

4.2.1. Biozone T5 (54.0–39.5 cm)

In this biozone, *Discostella stelligera* Cleve and Grunow dominates the diatom assemblage ($31.7 \pm 3.3\%$), followed by *Cocconeis placentula* (Ehrenberg) Cleve var. *lineata* ($18.0 \pm 2.4\%$) and *F. sensu lato* ($18.8 \pm 4.3\%$). Moreover, the contribution of *Gomphonema pumilum* (Grunow) Reichardt and Lange-Bertalot and *Aulacoseira granulata* (Ehrenberg) Simonsen represents only $6.3 \pm 1.3\%$ and $5.4 \pm 1.7\%$ of total diatom abundance, respectively. The sediments were characterized by a large fraction of mud ($81.8 \pm 4\%$) and to a lesser measure, by fine sand ($18.2 \pm 4\%$). The average composition of TOC and TN was $1.5 \pm 0.2\%$ and $0.14 \pm 0.02\%$, respectively, and the average atomic C/N ratio was 11.0 ± 1.2 . Average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were $-29.9 \pm 1.4\text{‰}$ and $1.9 \pm 0.8\text{‰}$, respectively (Fig. 4).

4.2.2. Biozone T4 (39.0–25.5 cm)

Cocconeis placentula var. *lineata* dominates this biozone with a mean relative abundance of $23.0 \pm 4\%$ of the assemblage. *Fragilaria sensu lato* ($22.0 \pm 6\%$) and *D. stelligera* ($19.5 \pm 5\%$) co-dominate the assemblage. Compared to biozone T5, the average contribution of *G. pumilum* and *A. granulata* increased to $7.7 \pm 2\%$ and $4.7 \pm 2\%$, respectively and was followed by *Navicula radiosa* Kützing with $4.1 \pm 2\%$ of the assemblage composition. The sediments were characterized by mud ($78.8 \pm 5\%$) and very fine sand ($21.2 \pm 5\%$). The average value of TOC and TN was $1.4 \pm 0.1\%$ and $0.12 \pm 0.02\%$, respectively. The average atomic C/N ratio was 11.7 ± 0.9 . The average values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were $-29.3 \pm 1.2\text{‰}$ and $1.95 \pm 0.6\text{‰}$, respectively (Fig. 4).

4.2.3. Biozone T3 (25.0–16.0 cm)

In this biozone, *F. sensu lato* represents $38.2 \pm 9\%$ of the relative abundance of this biozone, with an increasing trend toward the end of the biozone. *Discostella stelligera* is the co-dominant species, constituting $19.5 \pm 5\%$ of the assemblage. Compared to the biozone T4, *C. placentula* var. *lineata* significantly decreases in relative abundance from 23% to 13.4%, along with *G. pumilum* and *N. radiosa* that decreased from 7.7% to 2.3% and 4.1% to 1%, respectively. There is a modest contribution of *Achnanthis minutissimum* (Kützing) Czarnecki var. *minutissimum* (2.6%), *A. granulata* (4.8%), *Cymbella aspera* (Ehrenberg) Cleve (3.4%), *Cymbella tumida* (Brébisson in Kützing) van Heurck (3%). The sediment had the highest mud content of the entire core ($94.7 \pm 11\%$) and the lowest sand content ($5.3 \pm 11\%$). The average value of TOC and TN was $1.0 \pm 0.4\%$ and $0.06 \pm 0.03\%$ (respectively), while the average atomic C/N ratio was 16.3 ± 2.2 . Average values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were $-27.9 \pm 2.05\text{‰}$ and $4.9 \pm 1.4\text{‰}$, respectively (Fig. 4).

Table 3

List of diatom species that accounted for 95% of the total relative abundance in Core Tota0108. Life form (Pr = periphyton, Bt = benthic, Pl = plankton), pH (Ap = alkaliphile, Cn = Circumneutral, Ac = acidophile) and trophic state (Ol = oligotrophic, Me = mesotrophic, E = eutrophic, OE = oligotrophic/eutrophic). Criteria from Moro and Fürstenberger (1997) and Van Dam et al. (1994).

Code	Taxa	Habitat			pH			Trophic state			
		Pr	Bt	Pl	Ap	Cn	Ac	Ol	Me	E	OE
ACHDEXco	<i>Achnantheidium exiguum</i> var. <i>constrictum</i> (Grunow) Andresen, Stoermer and Kreis	+			+						+
ACHDMITmi	<i>A. minutissimum</i> (Kützing) Czarnecki var. <i>minutissimum</i>	+				+					+
ACCYNOo	<i>Actinocyclus normanii</i> (Gregory) Hustedt var. <i>normanii</i>			+	+					+	
AMRAOVAL	<i>Amphora ovalis</i> (Kützing) Kützing	+			+					+	
AUSEGRAN	<i>Aulacoseira granulata</i> (Ehrenberg) Simonsen			+	+					+	
CCNEPLi	<i>Cocconeis placentula</i> (Ehrenberg) Cleve var. <i>lineata</i>	+			+					+	
CYTEMENE	<i>Cyclotella meneghiniana</i> Kützing			+	+					+	
DSTESTEL	<i>Discostella stelligera</i> Cleve and Grunow			+			+				
CYLAASPE	<i>Cymbella aspera</i> (Ehrenberg) Cleve	+			+						+
CYLAGRAC	<i>C. graciliformis</i> Krammer			+	+					+	
CYLATUDA	<i>C. tumida</i> (Brébisson) Van Heurck	+			+					+	
DINEOVAL	<i>Diploneis ovalis</i> (Hilse) Cleve	+			+					+	
ENMAMINU	<i>Encyonema minutum</i> (Hilse) Mann		+			+				+	
ENMASILE	<i>Encyonema silesiacum</i> (Bleisch) Mann	+				+					+
EPITADNA	<i>Epithemia adnata</i> (Kützing) Brébisson			+	+					+	
EUTIMAJO	<i>Eunotia major</i> (Smith) Rabenhorst	+					+			+	
GONEPUMI	<i>Gomphonema pumilum</i> (Grunow) Reichardt and Lange-Bertalot	+			+						+
GONETRUN	<i>G. truncatum</i> var. <i>capitatum</i> (Ehrenberg) Patrick			+	+					+	
MERAVAAN	<i>Melosira varians</i> Agardh				+					+	
NAVIRAD	<i>Navicula radiosa</i> Kützing			+		+				+	
NITZPETA	<i>Nitzschia perminuta</i> (Grunow) Peragallo		+		+				+		
PLDILAFr	<i>Planolithidium frequentissimum</i> (Lange-Bertalot) Lange-Bertalot		+		+						+
PSRABRbr ^a	<i>Pseudostaurosira brevistriata</i> (Grunow) Williams and Round var. <i>brevistriata</i>		+		+						+
PSRABRin ^a	<i>P. brevistriata</i> var. <i>inflata</i> (Pantocsek) Hartley		+		+						+
RHOPGIBA	<i>Rhopalodia gibba</i> (Ehrenberg) Müller	+			+					+	
STRAve ^a	<i>Staurosira venter</i> (Ehrenberg) Kobayasi		+		+				+		
STLAPITA ^a	<i>Staurosirella pinnata</i> (Ehrenberg) Williams and Round		+		+						+
STLALEdu ^a	<i>S. leptostauron</i> var. <i>dubius</i> (Grunow) Edlund		+		+						+

^a *Fragilaria sensu lato* (*Pseudostaurosira brevistriata* var. *brevistriata*, *Pseudostaurosira brevistriata* var. *inflata*, *Staurosira venter*, *Staurosirella pinnata*, *Staurosirella leptostauron* var. *dubius*).

4.2.4. Biozone T2 (15.5–11.5 cm)

The assemblage is dominated by *F. sensu lato*, but in relation to the biozone T3, this species decreased in relative abundance from 38.2% to 31.8 ± 3%. Likewise, *D. stelligera* decreased in relative abundance from 22.2% to 12.1 ± 3%. We also observed the co-dominance of *C. placentula*

var. *lineata*, which increased in abundance from 13.4% to 16.0 ± 2%. Additionally, we found that *A. granulata* (13.4 ± 3%), *G. pumilum* (7.8 ± 3%) and *A. minutissimum* var. *minutissimum* (3.9 ± 5%) also increased in abundance. The sediments were characterized by mud (89.6 ± 15%) and very fine sand (10.4 ± 15%). The average value of TOC and TN was 1.5 ± 0.2%

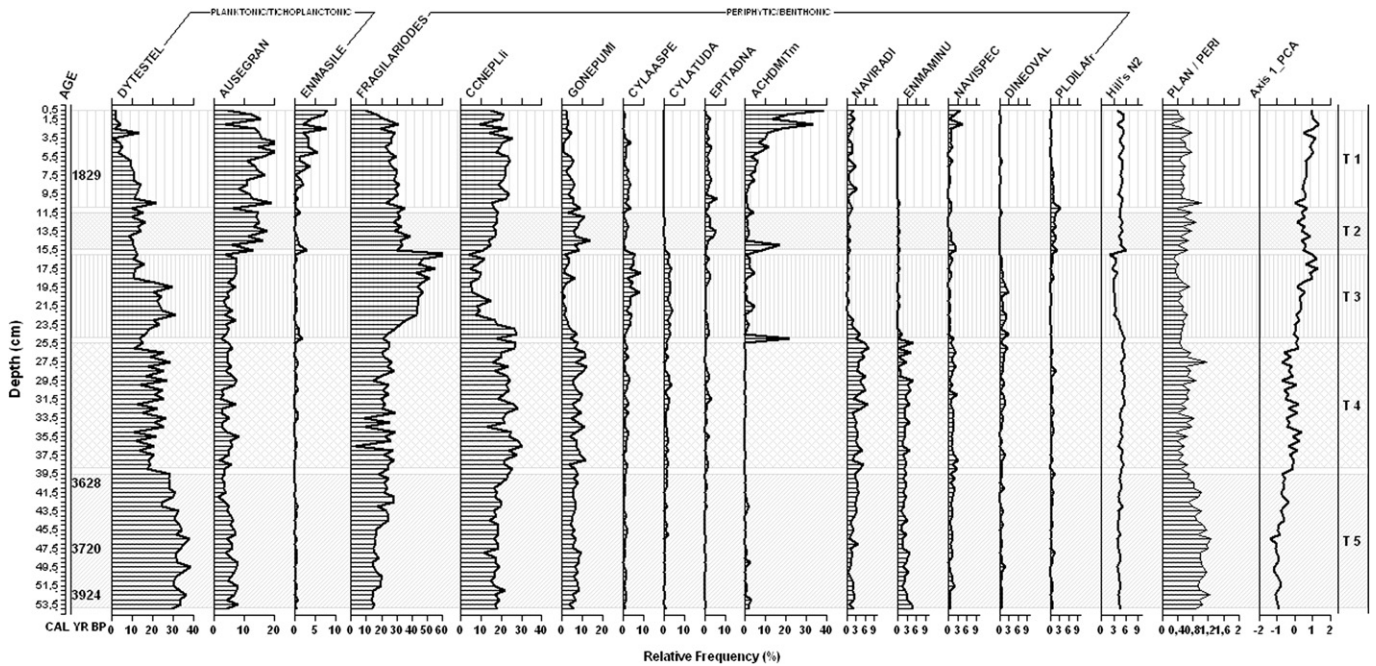


Fig. 3. Diagram of fossil diatoms species at the Tota0108 core. From left to right: Depth scale (cm), average of age range expressed in calibrated years BP (cal. yr BP), the most representative diatoms species are marked in the stratigraphic profile, Hill's N2 diversity, percentage of planktonics (Plan) and periphytics (Peri) species of the total sum of diatoms, eigenvalues of PCA1 explicability 46% and biozones are based on the CONISS dendrogram of the diatom record.

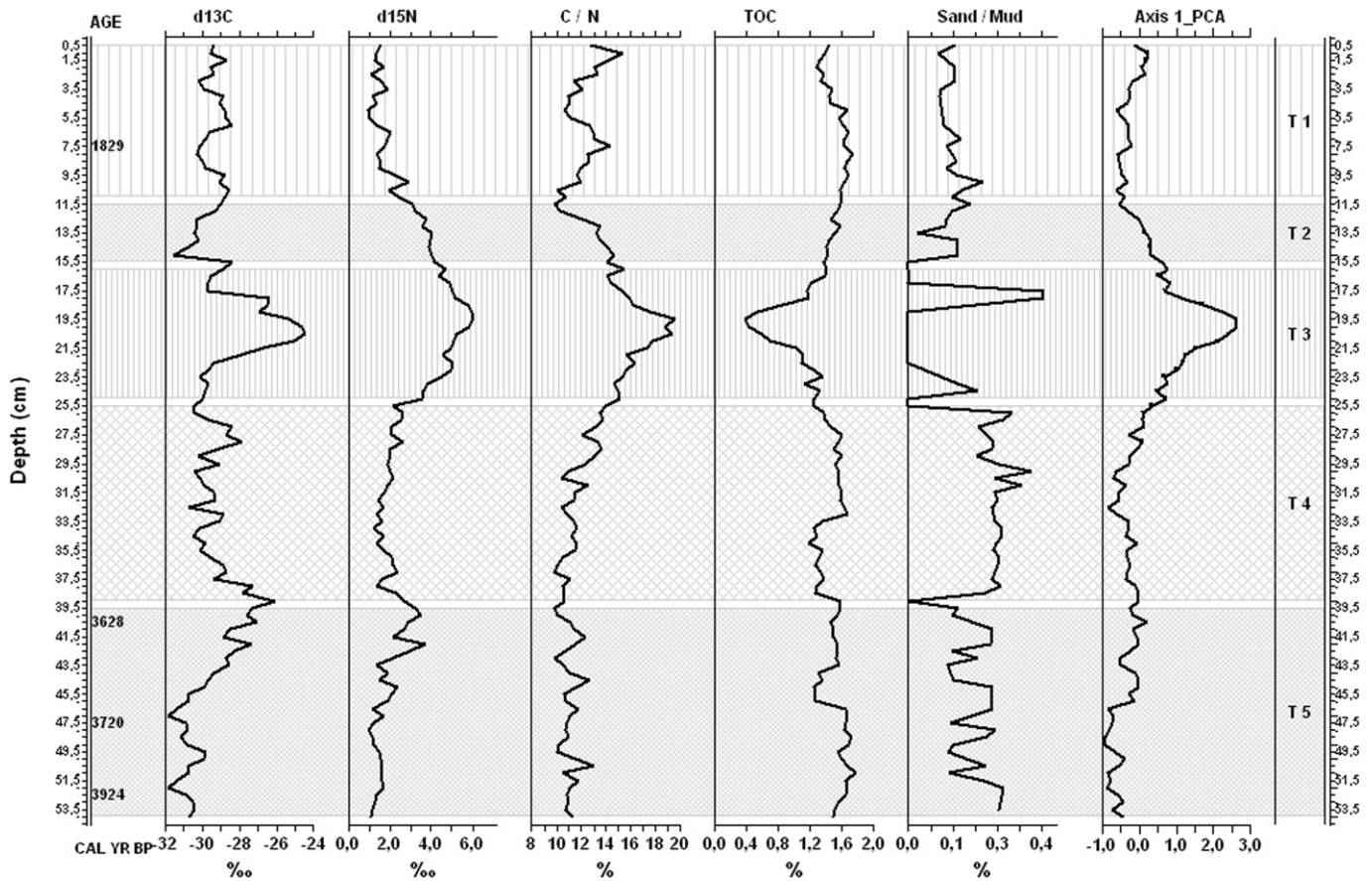


Fig. 4. Results from bulk organic geochemical and granulometry at the Tota0108 core. From left to right: Depth scale (cm), average of age range expressed in calibrated years BP (cal. yr BP), $\delta^{13}\text{C}$ isotope, $\delta^{15}\text{N}$ isotope, C/N ratio, total organic carbon (TOC) concentration, percentages of sand versus mud, eigenvalues of PCA1 explicability 56% and biozones are based on the CONISS dendrogram of the diatom record.

and $0.12 \pm 0.02\%$, respectively. The average atomic C/N ratio was 12.1 ± 0.8 . Average values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were $-30.01 \pm 1.7\%$ and $3.7 \pm 0.6\%$, respectively (Fig. 4).

4.2.5. Biozone T1 (11.0–0.5 cm)

Although *F. sensu lato* declined in abundance, fragilarioid diatoms dominate the assemblage of this biozone with $26 \pm 6\%$ of recorded abundance. The co-dominant species are *C. placentula* var. *lineata* with a relative abundance increasing from $16.0 \pm 2\%$ to $20.0 \pm 4\%$, from the base to the top of the biozone. *Discostella stelligera*, *A. granulata* and *G. pumilum* presented declining trends in their relative abundances. Of interest, *A. minutissimum* var. *minutissimum* is registered again in this biozone, however with abundance ($10.3 \pm 9.1\%$) bigger than in biozone T3. Other species that did not exceed 5% of the mean relative abundance are also present (e.g., *Encyonema silesiacum* (Hilse) Mann, *Epithemia adnata* (Kützing) Brébisson, *Actinocyclus normanii* (Gregory) Hustedt). The sediments were characterized by mud ($87.2 \pm 3.6\%$) and very fine sand ($12.8 \pm 3.6\%$). The average value of TOC and TN was $1.5 \pm 0.1\%$ and $0.13 \pm 0.02\%$, respectively. The average atomic C/N ratio was 12.3 ± 1.2 . The average values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were $-29.3 \pm 0.7\%$ and $1.6 \pm 1\%$, respectively (Fig. 4).

5. Discussion and conclusions

5.1. Paleolimnological characteristics of Lake Tota during the Holocene

The existence of the biozones implies that important changes occurred in the paleolimnology and paleohydrology of Lake Tota. These changes suggest that during the middle Holocene the lake

depth decreased, giving way to shallow waters at the end of the late Holocene.

In the base of the core, in biozone T5 (52.0–39.5 cm; 4014–3620 cal. yrs BP), diatom assemblages showed a typical environment of water deeper than the current level. This result is suggested by the dominance of planktonic species *D. stelligera*, together with *F. sensu lato* and *C. placentula* var. *lineata*. Diatom assemblages dominated by *D. stelligera* have been associated with thermally stable environments of cold, oligotrophic, alkaline conditions, displaying wide ranges in salinity. These assemblages tend to predominate at depths ranging between 5 and 25 m. These characteristics have been found in South American (Tapia et al., 2003; Hillyer et al., 2009) and North American aquatic ecosystems (Pienitz et al., 1995; Rühland et al., 2003; Moos et al., 2005) in Europe (Lotter and Bigler, 2000; Rioual et al., 2007) and Africa (Stone et al., 2010).

In relation to periphytic and benthic species, our results suggest that the dominance of the planktonic species *D. stelligera* indicates that the lake reached its maximum depth when the paleoclimate was characterized by its most humid period. Marchant et al. (2001b) recorded changes in Colombia vegetation from 4000 to 3500 ^{14}C years BP that were indicative of relatively wet climatic conditions resulting from increasing precipitation, decreasing evaporation, and/or shorter periods of drought. Vélez et al. (2006) describe that the fluctuations in the water level of Laguna Las Margaritas near its highest levels may be associated with climatic variability during the middle Holocene (3800 and 2600 ^{14}C years BP).

Discostella stelligera is associated with pristine ecosystem conditions, where it tends to dominate. According to Stone et al. (2010), the dominance of *D. stelligera* in Lake Malawi (Africa) occurred through a decrease in the concentration of nutrients due to the strengthening of

water column stratification, which is a result of the recent warming trend in the region. In a meta-analysis study, Rühland et al. (2003, 2008) associated the dominance of *D. stelligera* to warming climate and limnological changes (e.g., extended and/or more stable thermal stratification, increased nutrient cycling, high water transparency and neutral pH).

The granulometry indicates that during this period silty moderately sorted sediment accumulated. Because the core is situated near the Tobal River delta, this sorting probably corresponds to river hydrodynamics; the fine sediment indicates a relatively distal deltaic situation in agreement with the high water level implied by diatoms. Geochemical parameters (C/N ratio around 11; $\delta^{13}\text{C}$ of -32 (base) up to -27‰ (top) and $\delta^{15}\text{N}$ from 1 (base) to 3 (top)) and the relatively high total carbon accumulation are in good agreement with a phytoplanktonic production. Therefore, considering the hydrodynamics of the system and ecological interpretation, we conclude that in this period the lake was under the influence of a wetter climate that maintained a high discharge of Tobal River and a high water column of the lake.

In the following period, biozone T4 (39.0–25.5 cm; 3612–3076 cal. yrs BP), diatom assemblages were largely represented by *C. placentula* var. *lineata*, *D. stelligera* and *F. sensu lato*, with a predominant representation of *C. placentula* var. *lineata*. The ecological interpretation of *C. placentula* presented here is in the broad sense (*sensu lato*), due to lack of criteria to clearly differentiate between *C. placentula* var. *placentula*, *C. placentula* var. *euglypta* and *C. placentula* var. *lineata* (Romero and Jahn, 2013).

The changes in the life-form composition of diatom assemblages present in the sediment Tota0108 can be interpreted as an indication of changes in ecological conditions of the lake. Several reports have associated the presence of *C. placentula* with conditions of instability of physical and chemical conditions of lakes (Podritske and Gajewski, 2007; Ekdahl et al., 2008; Lami et al., 2010). Here, their dominance is associated with a high water level phase, occurring under a period of a warm and humid climate.

The fluctuation of water levels of lakes may lead to changes in various processes in the lake system, including the dissolution and fragmentation of valves, nutrient and light availability, variations in the stratification/circulation processes, oxygen levels, temperature, pH and biological interactions (Gell et al., 1994; Van Dam et al., 1994; Dearing, 1997; Stone and Fritz, 2004; Podritske and Gajewski, 2007; Wolin and Stone, 2010). The instability in these conditions would be beneficial to *C. placentula*, because it is considered an opportunistic species and resistant to disturbances (Veres et al., 1995). According to pollen studies, profiles from Colombian lake cores (Marchant et al., 2001a, 2002), fluctuations in lake levels recorded in the late Holocene may indicate increases in duration of the rainy season, keeping the weather humid in Colombia from 4000 to 3000 years BP.

The granulometric curves of this period are similar to those of biozone T5, however with a coarser particle size, easily visible in the sand/clay curve (Fig. 4). This change marks a gentle increase in hydrodynamics that may correspond to a lower lake level positioning the collection site closer to the delta and/or favoring littoral hydrodynamics. In this period, TOC was lower, in agreement with a lower lake level (Turcq et al., 2002), and C/N ratios increased, which could correspond to a higher influence of macrophytes.

In the core, the dominance of *C. placentula* var. *lineata* and geochemical characteristics of this period could indicate that the lake levels were low and linked to strong fluctuations of wet and dry periods, resulting from changes in the P/E balance in the lake basin. This pattern could determine the physical and chemical changes in water, favoring the dominance of this species.

Biozone T3 (25.0–16.0 cm; 3046–2445 cal. yrs BP) was dominated by the benthic species *F. sensu lato* and co-dominated by *D. stelligera* and *C. placentula* var. *lineata* (the valves at this stage were fragmented and dissolved). The high abundances of *F. sensu lato*, especially the species *S. pinnata*, occur concomitantly with low diversity (Hill's N_2) (Fig. 2).

Most taxa of *F. sensu lato* are adapted to and compete well in fluctuating environmental conditions (Schmidt et al., 2004). Accordingly, these species can be competitive in nutrient-poor, cold, alkaline and shallow (<8 m) environments when compared to planktonic diatoms under similar conditions (Brugam et al., 1998; Lotter and Bigler, 2000; Rühland et al., 2003; Finkelstein and Gajewski, 2008).

The low diversity (Hill's N_2) and the dominance of fragilarioids can be explained by a reduction in the water column depth, providing a higher representation (%) of benthic species in relation to the deposition of planktonic species (Wolin and Stone, 2010). On the other hand, other studies have identified an increase in the percentage representation of species in benthic assemblages of diatoms with the increasing water level of lakes, because in some lakes, the increased water column allows macrophyte colonization of larger areas (Stone and Fritz, 2004). Therefore, this macrophyte-rich region provides greater export of benthic species to close-by regions of the lake floor, reducing the signal of planktonic ones.

Sedimentation during this period is quite different from others. The sediments are fine and poorly sorted, multimodal, and demonstrating low hydrodynamics. The C/N ratio is higher, indicating an increase in macrophytic contribution. Our hypothesis is that, at that time, the site was separated from the lake open-water by a macrophyte bank. The lower may TOC indicate an elevated degradation of organic matter in an environment close to the lake margin, possibly with seasonal or interannual drying. The higher $\delta^{13}\text{C}$ values indicate contributions of grass, probably developing on the lake margin in seasonally emerged areas. The high $\delta^{15}\text{N}$ well corresponds to an environment exposed to periodic droughts (Martinelli et al., 1999).

The ecology of the diatom species as well as geochemical and granulometric information from the sediments of Core Tota0108 suggest that Lake Tota – Sector Lake Chico – presents a lower lake level than the previous biozones, reflecting a periodic influence from dry and cold climate certainly related to a reduction in precipitation. This interpretation agrees with Vélez et al. (2006), who attributed the low levels of Las Margaritas and Fúquene lakes to dry climates during the period of 4180–2750 years BP.

When comparing biozone T2 (15.5–11.5 cm; 2408–2107 cal. yrs BP) to other biozones in the core, we observed a slight increase in *A. granulata* and *C. placentula*, concomitantly with a decrease in *F. sensu lato*. This change in diatom assemblage structure may be associated with conditions of high variability in water temperature, depth and circulation, that may have altered the prevailing chemical conditions (Battarbee et al., 2001; Rühland and Smol, 2005; Rioual et al., 2007). According to Reynolds (1993), Rioual et al. (2007), Stone et al. (2010), and Wolin and Stone (2010), most of the *Aulacoseira* spp. (particularly *A. granulata* and related taxa) have highly silicified valves and therefore display high rates of sinking and sedimentation, such that intense turbulence is required to keep *Aulacoseira* in the euphotic zone of lakes. Thus, the presence of the *Aulacoseira* spp. indicates its inclusion in polymictic lakes.

Low $\delta^{13}\text{C}$, high TOC, and lowering of the C/N ratio and $\delta^{15}\text{N}$ together with granulometric curves similar to the base of the core suggest that this period is characterized by the return of river hydrodynamic influence. Higher amounts of clay may correspond to a water column deeper than during biozone T5, if the dominant factor was littoral dynamics. The same higher amounts of clay may be connected with a lower river discharge, if the river discharge governs the sedimentological process. This later interpretation agrees better with the diatom data. Therefore, we conclude from the geochemical characteristics and the presence of *A. granulata* that the lake increased in water level, while high mixing occurred and was associated with high water level fluctuations. These conditions could be the result of the influence of a humid and windy climate.

Results from biozone T5 (11.0–0.5 cm; 2068 cal. yrs BP to the present day) suggest strong fluctuations in lacustrine characteristics, such as deeper water (well above the site of the core collection) becoming

gradually shallower with time. This interpretation can be inferred from the change of planktonic to epiphytic species. *Achnanthydium minutissimum* var. *minutissimum* dominates the top of the core and is associated with *C. placentula* var. *lineata* and *E. silesiacum*, along with low abundance of *A. granulata*, *D. stelligera* and *S. pinnata*. Today, this diatom assemblage inhabits the littoral zone of Tota Lake (Cardozo et al., 2005).

Achnanthydium minutissimum var. *minutissimum* is recorded as periphytic and epiphytic (Van Dam et al., 1994); this species is typical of shallow lakes with a well-developed coastal zone and high biological productivity, favoring the establishment of periphytic communities (i.e., epiphytes) (Hassan et al., 2009). The presence of this colonizing species is characteristic of disturbed environments that are subjected to strong currents and turbulence (Peterson and Stevenson, 1992; Ekdahl et al., 2008). This species is commonly found in well-oxygenated water (Caballero et al., 2006) with relatively high TN and specific conductivity values (Keatley et al., 2006) and with high concentrations of dissolved organic carbon (DOC) (Rühland et al., 2003).

In this period, the Tota Lake core has lower clay values than during the preceding period. The TOC values are high and similar to biozone T1. The C/N ratio shows high values that can be interpreted as high phytoplankton and macrophyte contributions. These results, along with the presence of *A. minutissimum* var. *minutissimum*, suggest that the lake could have been strongly influenced by both lake littoral and Toba River dynamics. Furthermore, this suggests that the site was influenced by heavy rains, which slowly reduced in intensity up to present day values.

Based on the paleolimnological diatom assemblage reconstructions, granulometry and geochemical data, we conclude that the pattern of rainfall in Lake Tota was influenced by the regime of Llanos Orientales and shows a similar behavior in terms of precipitation patterns recorded in Las Margaritas Lake – Llanos Orientales (Vélez et al., 2006). The Tota Lake results may be explained by changes in the position of the ITCZ. During the late Holocene the ITCZ shifted southwards, causing drier climates in northern South America and more humid conditions in the Amazon (e.g., Martin et al., 1997; Haug et al., 2001). The Llanos Orientales, including the Las Margaritas location, became wetter as the southeast Trade Winds accumulated moisture while crossing the Amazon region. This accumulated moisture was brought to the eastern Colombia regions during the boreal summer season, during which the ITCZ had less humidifying effect on the site (Vélez et al., 2006).

6. Paleoclimate inferences

A period of high lake level is observed at Tota Lake from 4000 to 3620 cal. yrs BP. This wet phase is also registered in Paramo de Frontino (Velásquez and Hooghiemstra, 2013) and other sites in Colombia (e.g. Marchant et al., 2001a). Mid to late Holocene increases in precipitation is observed in several regions in tropical South America (Wanner et al., 2008; Bird et al., 2011; Prado et al., 2013). Bird et al. (2011) have interpreted this phenomenon as a large scale trend of South America Monsoon (SAM) in both hemispheres. Although a SAM increase would increase rainfall in a large part of the Amazon Basin, a rainfall increase in our region would need a transport of this wetness to the north (Poveda et al., 2006). SAM precipitation occurs from December to February while the rainfalls in northern regions of South America, where Tota Lake is located, are from June to August (Cañón and Valdes, 2011). It therefore seems difficult that a SAM increase would increase precipitation in both southern and northern South American tropics. Behling and Hooghiemstra (2000) suggest that the transition from dry to humid conditions could be related to a change in the latitudinal range of the annual migration of the ITCZ. Indeed the Cariaco record indicates that a southward shift of the ITCZ northern position occurred between 4300 and 3700 cal. yrs BP (Haug et al., 2001). On the southern border of the ITCZ latitudinal range there is a decrease of precipitation in northeast Brazil from 5000 to 4200 cal. yrs BP (Cruz et al., 2009). This decrease suggests

a northern migration of the ITCZ southern limit (Silva Dias et al., 2009) and then, together with the southward migration of the northern limit, a narrowing of the ITCZ latitudinal range. Such a condition would have favored an increase of Trade Wind intensity at the latitude range of our site, increasing water vapor transfer and precipitation.

The lowest lake level of the late Holocene in Tota Lake is attained during the 3046–2445 cal. yrs BP interval. There are strong variations of precipitation at that time in the Cariaco record (Haug et al., 2001) that have been interpreted as related to El Niño events. In Pallacocha Lake (Ecuador), the period from 3400 to 2500 yrs BP is characterized by a high density of clastic laminae interpreted as repeated occurrences of El Niño events (Moy et al., 2002). The southwest shift of the rain region to Ecuador during El Niño events may explain the low lake levels in Tota. But in the llanos Orientales the forest kept developing during this period. At Loma Linda Lake (Behling and Hooghiemstra, 2000), the forest maximum is reached between 2600 and 2000 cal. yrs BP; however a decrease in the planktonic algae *Botryococcus* began at 3800 cal. yrs BP. From these considerations, it seems possible that the repetitive occurrences of El Niño events would have had more impact on the levels of the lakes than on the vegetation in this region.

Acknowledgements

We would like to thank CNPq (Brazil) and Colciencias (Colombia) for funding the project of international cooperation ECLIPSE–CNPq N° 490208/2007–0, the master scholarship granted by CNPq N° 135252/2009–1 to the first author, and the project ANR 2010 BLANC 608 01 – EL PASO. Thanks also to Corpoboyacá, especially Beatriz Perez and Carlos Eduardo Montaña, Professor Dr. Nelson Javier Aranguren Riaño – UPTC – for helping with the field logistics, Dr. João C. Viana Cerqueira – UFF for helping with the laboratory logistics, students Renato Silva and Everton Santos for collaboration in analyses of sediments of Tota0108 core, Dr. Antoine Leduc for helping in English revision, the “Núcleo de Estudos Ambientais” by loan of particle analyzer CILAS (Mod.1064), and the staff of the Benthic Ecology Laboratory at UFBA – Brazil. We are also grateful to the two anonymous reviewers for their comments that helped us improve this paper.

References

- Abbott, M.B., Wolfe, B.B., Aravena, R., Wolfe, A.P., Seltzer, G.O., 2000. Holocene hydrological reconstructions from stable isotopes and paleolimnology, Cordillera Real, Bolivia. *Quat. Sci. Rev.* 19, 1801–1820.
- Allen, J.R., Thornley, D.M., 2004. Laser granulometry of Holocene estuarine silts: effects of hydrogen peroxide treatment. *Holocene* 14, 290–295.
- Andreola, F., Castellini, E., Manfredini, T., Romagnoli, M., 2004. The role of sodium hexametaphosphate in the dissolution process of kaolinite and kaolin. *J. Eur. Ceram. Soc.* 24, 2113–2124.
- Aranguren-Riaño, N., Guisande, C., Ospina, R., 2011. Factors controlling crustacean zooplankton species richness in Neotropical lakes. *J. Plankton Res.* 33, 1–9.
- Battarbee, R.W., 1986. Diatom analysis. In: Berglund, B.E. (Ed.), *Handbook of Holocene Palaeoecology and Palaeohydrology*. J. Wiley, Chichester, pp. 527–570.
- Battarbee, R.W., 2000. Palaeolimnological approaches to climate change, with special regard to the biological record. *Quat. Sci. Rev.* 19, 107–124.
- Battarbee, R.W., Jones, V.J., Flower, R.J., Cameron, N.G., Bennion, H., Carvalho, L., Juggins, S., 2001. Diatoms. In: Smol, J.P., Birks, H.J., Last, W.M. (Eds.), *Tracking Environmental Change Using Lake Sediments. Terrestrial, Algal and Siliceous Indicators*, 3. Kluwer Academic Publishers, The Netherlands, pp. 155–202.
- Behling, H., Hooghiemstra, H., 1998. Late Quaternary palaeoecology and palaeoclimatology from pollen records of the savannas of the Llanos Orientales in Colombia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 139, 251–267.
- Behling, H., Hooghiemstra, H., 1999. Environmental history of the Colombian savannas of the Llanos Orientales since the Last Glacial Maximum from lake records El Piñal and Carimagua. *J. Paleolimnol.* 21, 461–476.
- Behling, H., Hooghiemstra, H., 2000. Holocene Amazon rain-forest savanna dynamics and climatic implications: high-resolution pollen record from Laguna Loma Linda in eastern Colombia. *J. Quat. Sci.* 15, 687–695.
- Bennett, K.D., 1996. Determination of the number of zones in a biostratigraphical sequence. *New Phytol.* 132, 155–170.
- Bird, B.W., Abbott, M.B., Rodbell, D.T., Vuille, M., 2011. Holocene tropical South American hydroclimate revealed from a decadal resolved lake sediment $\delta^{18}\text{O}$ record. *Earth Planet. Sci. Lett.* 310, 192–202.
- Birks, H.J., 1998. Numerical tools in paleolimnology – progress, potentialities, and problems. *J. Paleolimnol.* 20, 1307–1332.

- Birks, H.H., Birks, H.J., 2006. Multi-proxy studies in palaeolimnology. *Veg. Hist. Archaeobot.* 15, 235–251.
- Brugam, R.B., McKeever, K., Kolesa, L., 1998. A diatom-inferred water depth reconstruction for Upper Peninsula, Michigan, lake. *J. Paleolimnol.* 20, 267–276.
- Caballero, M., Vázquez, G., Lozano-García, S., Rodríguez, A., Sosa-Nájera, S., Ruiz-Fernández, A.C., Ortega, B., 2006. Present limnological conditions and recent (ca. 340 yr) palaeolimnology of a tropical lake in the Sierra de Los Tuxtlas, eastern Mexico. *J. Paleolimnol.* 35, 83–97.
- Cañón, J., 2001. Balance hidrológico del lago tota y estudio preliminar del comportamiento hidráulico en lagos. (Tesis de maestría) Universidad Nacional de Colombia, Bogotá, Colombia.
- Cañón, J., Valdes, J., 2011. Assessing the influence of global climate and anthropogenic activities on the water balance of an Andean Lake. *J. Water Resour. Prot.* 3, 883–891.
- Cardozo, A.Y., Pita, S., 2004. Estudio de la estructura cualitativa y cuantitativa de la comunidad fitoplanctónica del lago de Tota. Sector Lago Chico (Aquitania-Boyacá). (Tesis de pregrado) Universidad Pedagógica y Tecnológica de Colombia, Tunja, Colombia.
- Cardozo, A.Y., Bermúdez, A., Aranguren, N., Duque, S.R., 2005. Algas planctónicas del lago de Tota: listado taxonómico actualizado. *Cienc. Desarro.* 2, 80–88.
- Cruz, F.W., Vuille, M., Burns, S.J., Wang, X., Cheng, H., Werner, M., Edwards, R.L., Karmann, I., Auler, A.S., Nguyen, H., 2009. Orbitally driven east–west antiphasing of South American precipitation. *Nat. Geosci.* 2, 1–5.
- Dearing, J.A., 1997. Sedimentary indicators of lake-level changes in the humid temperate zone: a critical review. *J. Paleolimnol.* 18, 1–14.
- Ekdahl, E.J., Fritz, S.C., Baker, P.A., Riggsby, C.A., Coley, K., 2008. Holocene multidecadal-to millennial scale hydrologic variability on the South American Altiplano. *Holocene* 18, 867–876.
- Finkelstein, S.A., Gajewski, K., 2008. Responses of Fragilaroid-dominated diatom assemblages in a small Arctic lake to Holocene climatic changes, Russell Island, Nunavut, Canada. *J. Paleolimnol.* 40, 1079–1095.
- Gell, P.A., Barker, P.A., De Deckker, P., Last, W.M., Jelicic, L., 1994. The Holocene history of West Basin lake Victoria, Australia: chemical changes based on fossil biota and sediment mineralogy. *J. Paleolimnol.* 12, 235–258.
- González, A.A., Aranguren-Riaño, N., Gaviria, S., 2008. Cambios en la estructura de la población de *Boeckella gracilis* (Crustacea, Centropagidae) en el plancton del lago de tota, Boyacá – Colombia. *Acta Biol. Colomb.* 13, 61–72.
- Gray, A.B., Pasternack, G.B., Watson, E.B., 2010. Hydrogen peroxide treatment effects on the particle size distribution of alluvial and marsh sediments. *Holocene* 20, 293–301.
- Grimm, E.C., 1987. Coniss: a Fortran 77 program for stratigraphically constraining cluster analysis by the method of the incremental sum of square. *Comput. Geosci.* 13, 13–35.
- Hassan, G.S., Tietze, E., De Francesco, C.G., 2009. Modern diatom assemblages in surface sediments from shallow lakes and streams in southern Pampas (Argentina). *Aquat. Sci.* 71, 487–499.
- Haug, G., Hughen, K., Sigman, D., Peterson, L., Röhl, U., 2001. Southward migration of the Intertropical Convergence Zone through the Holocene. *Science* 293, 1304–1307.
- Hydroestudios Ltda., 1978. Estudio de conservación y manejo del lago de Tota y su cuenca. Corporación Autónoma Regional CAR, Fonade, Bogotá.
- Hill, M.O., Gauch, H.G., 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetation* 42, 47–58.
- Hillyer, R., Valencia, B.G., Bush, M.B., Silman, M.R., Steinitz-Kannan, M., 2009. A 24 700-year paleolimnological history from the Peruvian Andes. *Quat. Res.* 71, 71–82.
- Hustedt, F., 1961–1969. Die Kieselalgen Deutschlands, Österreich und der Schweiz (three volumes). In: Rabenhorst, L. (Ed.), *Kryptogamen flora van Deutschland, Österreich and der Schweiz Band 7.1, 7.2, 7.3*. Akademische Verlagsgesellschaft, Keipzig, Alemania.
- Izurrieta, X., 2007. Estrategia de humedales altoandinos. In: Castro, M., Fernández, L. (Eds.), *Gestión sostenible de humedales*. Programa Iberoamericano de Ciencia y Tecnología para el Desarrollo and Universidad de Chile, Santiago de Chile, pp. 173–183.
- Juggins, S., 2007. C2 Version 1.5 User guide. Software for Ecological and Palaeoecological Data Analysis and Visualisation. Newcastle University, Newcastle upon Tyne, UK, p. 73.
- Juggins, S., 2009. Rioja an R package for the analysis of quaternary science data. New Castle, UK. <http://cran.r-project.org/package=r.ioja>.
- Keatley, B., Douglas, M.S., Smol, J.P., 2006. Early-20th century environmental changes inferred using diatoms from a small pond on Melville Island, NWT, Canadian High Arctic. *Hydrobiologia* 553, 15–26.
- Lami, A., Marchetto, A., Salerno, F., Tartari, G., Guilizzoni, P., Rogora, M., Tartari, G., 2010. Chemical and biological response of two small lakes in the Khumbu Valley, Himalayas (Nepal) to short-term variability and climatic change as detected by long-term monitoring and paleolimnological methods. *Hydrobiologia* 648, 189–205.
- Lepš, J., Šmilauer, P., 2003. *Multivariate Analysis of Ecological Data Using CANOCO*. Cambridge University Press, Cambridge, p. 269.
- Lotter, A.F., Bigler, C., 2000. Do diatoms in the Swiss Alps reflect the length of ice-cover? *Aquat. Sci.* 62, 125–141.
- Lotter, A.F., Birks, H.J., 2003. The Holocene palaeolimnology of Sägistalsee and its environmental history – a synthesis. *J. Paleolimnol.* 30, 333–342.
- Maldonado, M., Maldonado-Ocampo, J.O., Ortega, H., Encalada, A.C., Carvajal-Vallejos, F.M., Rivadeneira, J.F., Acosta, F., Jacobsen, D., Crespo, A., Rivera-Rondón, C. A., 2011. Biodiversity in aquatic systems of the tropical Andes. In: Herzog, S., Martínez, R., Jørgensen, P., Tiessen, H. (Eds.), *Climate Change and Biodiversity in the Tropical Andes*. Inter American Institute for Global research (IAI) and Scientific Committee on Problems of the Environment (SCOPE), p. 348.
- Marchant, R., Behling, H., Berrio, J.C., Cleef, A., Duivenvoorden, J., Hooghiemstra, H., Kuhry, P., Melief, B., Van Geel, B., Vander Hammen, T., Van Reenen, G., Wille, M., 2001a. Mid to Late-Holocene pollen-based biome reconstructions for Colombia. *Quat. Sci. Rev.* 20, 1289–1308.
- Marchant, R., Berrio, J.C., Cleef, A., Duivenvoorden, J., Van Geel, B., Van der Hammen, T., Hooghiemstra, H., Kuhry, P., Melief, B.M., Van Reenen, G., Wille, M., 2001b. A reconstruction of Colombian biomes derived from modern pollen data along an altitude gradient. *Rev. Palaeobot. Palynol.* 117, 79–92.
- Marchant, R., Behling, H., Berrio, J.C., Cleef, A., Duivenvoorden, J., Hooghiemstra, H., Kuhry, P., Melief, B., Van Geel, B., Vander Hammen, T., Van Reenen, G., Wille, M., 2002. Pollen-based biome reconstructions for Colombia at 3000, 6000, 9000, 12,000, 15,000 and 18,000 ¹⁴C yr ago: Late Quaternary tropical vegetation dynamics. *J. Quat. Sci.* 17, 113–129.
- Marengo, J.A., Pabón, J.D., Díaz, A., Rosas, G., Ávalos, G., Montealegre, E., Villacis, M., Solman, S., Rojas, M., 2011. Climate change: evidence and future scenarios for the Andean region. In: Herzog, S.K., Martínez, R., Jørgensen, P.M., Tiessen, H. (Eds.), *Climate Change and Biodiversity in the Tropical Andes*. Inter-American Institute for Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE), pp. 110–127.
- Martin, L., Bertaux, J., Corregge, T., Ledru, M., Mourguiart, Ph., Sifeddine, A., Soubies, F., Wirmann, D., Suguio, K., Turcq, B., 1997. Astronomical forcing of contrasting rainfall changes in tropical South America between 12,400 and 8800 cal yr. B.P. *Quat. Res.* 47, 117–122.
- Martínez, R., Ruiz, D., Andrade, M., Blacutt, L., Pabón, D., Jaimes, E., León, G., Villacis, M., Quintana, J., Montealegre, E., Euscátegui, C., 2011. Synthesis of the climate of the tropical Andes. In: Herzog, S.K., Martínez, R., Jørgensen, P.M., Tiessen, H. (Eds.), *Climate Change and Biodiversity in the Tropical Andes*. Inter-American Institute for Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE), pp. 97–109.
- Mason, I.M., Guzkowska, M.A., Rapley, C.G., 1994. The response of lake levels and are as to climatic change. *Clim. Change* 27, 161–197.
- Martinelli, L.A., Piccolo, M.C., Townsend, A.R., Vitousek, E.M., Cuevas, E., McDowell, W., Robertson, G.P., Santos, O.C., Treseder, K., 1999. Nitrogen stable isotopic composition of leaves and soil: tropical versus temperate forests. *Biogeochemistry* 46, 45–65.
- McCormac, F.G., Hogg, A.G., Blackwell, P.G., Buck, C.E., Higham, T.F., Reimer, P.J., 2004. SHCal04 southern hemisphere calibration 0–11.0 cal kyr BP. *Radiocarbon* 46, 1087–1092.
- McCune, B., Grace, J.B., Urban, D.L., 2002. *Analysis of Ecological Communities*. Gleden Beach, Oregon, p. 284.
- Metzeltin, D., Lange-Bertalot, H., 1998. Tropical diatoms of South America. *Iconogr. Diatomol.* 5, 1–695.
- Metzeltin, D., Lange-Bertalot, H., Garcia-Rodriguez, F., 2005. Diatoms of Uruguay. *Iconogr. Diatomol.* 15, 1–737.
- Monroy, D., 2003. Variación espacio temporal de los crustáceos planctónicos del lago de Tota Boyacá – Colombia. (Tesis de pregrado) Universidad Pedagógica y Tecnológica de Colombia, Tunja, Colombia.
- Moos, M.T., Laird, K.R., Cumming, B.F., 2005. Diatom assemblages and water depth in Lake 239 (Experimental Lakes Area, Ontario): implications for paleoclimatic studies. *J. Paleolimnol.* 34, 217–227.
- Moro, R.S., Fürstenberger, C.B., 1997. Catálogo dos principais parâmetros ecológicos de diatomáceas não-marinhas. Universidade Estadual Ponta Grossa, Ponta Grossa, Brasil, p. 282.
- Moy, C.M., Seltzer, G.O., Rodbell, D.T., Anderson, D.M., 2002. Variability of El Niño/Southern Oscillation activity at millennial timescales during the Holocene Epoch. *Science* 296, 162–165.
- Patrick, R., Reimer, C.W., 1966. *The Diatoms of the United States Exclusive of Alaska and Hawaii*. Fragilariaceae, Eunotiaceae, Achnantheaceae, Naviculaceae. Monographs 13, vol. 1. Academy of Natural Sciences, Philadelphia, p. 688.
- Peterson, C.G., Stevenson, R.J., 1992. Resistance and resilience of lotic algal communities: importance of disturbance timing and current. *Ecology* 73, 1445–1461.
- Pienitz, R., Smol, J.P., Birks, H.J., 1995. Assessment of freshwater diatoms as quantitative indicators of past climatic change in the Yukon and Northwest Territories, Canada. *J. Paleolimnol.* 13, 21–49.
- Podrifske, B., Gajewski, K., 2007. Diatom community response to multiple scales of Holocene climate variability in a small lake on Victoria Island, NWT, Canada. *Quat. Sci. Rev.* 26, 3179–3196.
- Poveda, G., Waylen, P.R., Pulwarty, R.S., 2006. Annual and inter-annual variability of the present climate in northern South America and southern Mesoamerica. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 234, 3–27.
- Prado, L.F., Wainer, I., Chiessi, C.M., Ledru, M.P., Turcq, B., 2013. A Mid-Holocene climate reconstruction for eastern South America. *Clim. Past* 9, 2117–2133.
- R Development Core Team, 2009. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria (<http://www.R-project.org>).
- Reynolds, C.S., 1993. *The Ecology of Freshwater Phytoplankton*. Cambridge University Press, Cambridge, p. 384.
- Rioual, P., Andrieu-Ponel, V., Beaulieu, J.L., Reille, M., Svobodovac, H., Battarbee, R. W., 2007. Diatom responses to limnological and climatic changes at Ribains Maar (French Massif Central) during the Eemian and Early Würm. *Quat. Sci. Rev.* 26, 1557–1609.
- Romero, O.E., Jahn, R., 2013. Typification of *Cocconeis lineata* and *Cocconeis euglypta* (Bacillariophyta). *Diatom Res.* 28, 175–184.
- Round, F.E., Crawford, R.M., Mann, D.G., 1990. *The Diatoms: Biology and Morphology of the Genera*. Cambridge University Press, Cambridge, p. 747.
- Rühland, K., Priesnitz, A., Smol, J.P., 2003. Paleolimnological evidence from diatoms for recent environmental changes in 50 lakes across Canadian arctic treeline. *Arct. Antarct. Alp. Res.* 35, 110–123.
- Rühland, K., Smol, J.P., 2005. Diatom shifts as evidence for recent Subarctic warming in a remote tundra lake, NWT, Canada. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 226, 1–16.
- Rühland, K., Paterson, A., Smol, J.P., 2008. Hemispheric-scale patterns of climate-related shifts in planktonic diatoms from North American and European lakes. *Glob. Chang. Biol.* 14, 1–15.

- Sakamoto, M.S., Ambrizzi, T., Poveda, G., 2011. Moisture sources and life cycle of convective systems over western Colombia. *Adv. Meteorol.* <http://dx.doi.org/10.1155/2011/890759> (Article ID 890759, 11 pages).
- Schmidt, R., Kamenik, C., Lange-Bertalot, H., Klee, R., 2004. *Fragilaria* and *Staurosira* (Bacillariophyceae) from sediment surfaces of 40 lakes in the Austrian Alps in relation to environmental variables, and their potential for paleoclimatology. *J. Limnol.* 63, 171–189.
- Silva Dias, P.L., Turcq, B., Dias, M.A.F.S., Braconnot, P., Jorgetti, T., 2009. Mid-Holocene climate of tropical South America: a model-data approach. *Past Climate Variability in South America and Surrounding Regions. Developments in Paleoenvironmental Research*, 14, pp. 259–281.
- Smol, J.P., 2002. Pollution of lakes and rivers. *A Paleolimnological Perspective*. Arnold, London, p. 280.
- Stone, J.R., Fritz, S.C., 2004. Three-dimensional modeling of lacustrine diatom habitat areas: improving paleolimnological interpretation of planktic:benthic ratios. *Limnol. Oceanogr.* 49, 1540–1548.
- Stone, J., Westover, K., Cohen, A., 2010. Late Pleistocene paleohydrography and diatom paleoecology of the central basin of Lake Malawi, Africa. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 303, 51–70.
- Stuiver, M., Reimer, P.J., Reimer, R.W., 2005. CALIB 5.0 program and documentation [online]. Available from: <http://calib.qub.ac.uk/calib/> (Accessed 2011).
- Tapia, P.M., Fritz, S.C., Baker, P.A., Seltzer, G.O., Dunbar, R.B., 2003. A Late Quaternary diatom record of tropical climatic history from Lake Titicaca (Peru and Bolivia). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 194, 139–164.
- Turcq, B., Cordeiro, R.C., Albuquerque, A.L.S., Sifeddine, A., Simões Filho, F.F.L., Souza, A.G., Abrão, J.J., Oliveira, F.B.L., Silva, A.O., Capitâneo, J.A., 2002. Accumulation of organic carbon in five Brazilian lakes during the Holocene. *Sediment. Geol.* 148, 319–342.
- Vaasma, T., 2008. Grain – size analysis of lacustrine sediments: a comparison of pre-treatment methods. *Est. J. Ecol.* 57, 231–243.
- Van Dam, H., Mertens, A., Sinkeldam, J., 1994. A coded checklist and ecological indicator values of freshwater diatoms from the Netherlands. *Neth. J. Aquat. Ecol.* 28, 117–133.
- Van Der Hammen, T., Hooghiemstra, H., 2000. Neogene and Quaternary history of vegetation, climate, and plant diversity in Amazonia. *Quat. Sci. Rev.* 19, 725–742.
- Van't Veer, R., Islebe, G., Hooghiemstra, H., 2000. Climatic change during the Younger Dry as chron in northern South America: a test of the evidence. *Quat. Sci. Rev.* 19, 1821–1835.
- Velásquez, C.A., Hooghiemstra, H., 2013. Pollen-based 17-kyr forest dynamics and climate change from the Western Cordillera of Colombia; no-analogue associations and temporarily lost biomes. *Rev. Palaeobot. Palynol.* 194, 38–49.
- Vélez, M.I., Wille, M., Hooghiemstra, H., Metcalfe, S., Vanderberghe, J., Van der Borg, K., 2001. Late Holocene environmental history of southern Chocó region, Pacific Colombia, sediment, diatom and pollen analysis of core El Caimito. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 173, 197–214.
- Vélez, M.I., Hooghiemstra, H., Metcalfe, S., Martínez, I., Mommersteeg, H., 2003. Pollen and diatom based environmental history since the Last Glacial Maximum from the Andean core Fúquene-7, Colombia. *J. Quat. Sci.* 18, 17–30.
- Vélez, M.I., Berrío, J.C., Hooghiemstra, H., Metcalfe, S., 2005a. Palaeoenvironmental changes during the last ca.8529 cal yr in the dry Forest ecosystem of the Patía Valley. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 216, 279–302.
- Vélez, M.I., Wille, M., Hooghiemstra, H., Metcalfe, S., 2005b. Integrated diatom-pollen based reconstruction of environmental change from Laguna Las Margaritas in the western Colombian savanna area. *Holocene* 15, 1184–1198.
- Vélez, M.I., Hooghiemstra, H., Metcalfe, S., Wille, M., Berrío, J., 2006. Late Glacial and Holocene environmental and climatic changes from a limnological transect through Colombia, northern South America. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 234, 81–96.
- Veres, A.J., Pienitz, R., Smol, J.P., 1995. Lake water salinity and periphytic diatom succession in three Subarctic lakes, Yukon Territory, Canada. *Arctic* 48, 63–70.
- Wanner, H., Beer, J., Butikofer, J., Crowley, T.J., Cubasch, U., Flückiger, J., Goosse, H., Grosjean, M., Joos, F., Kaplan, J.O., Kuttel, M., Müller, S.A., Prentice, I.C., Solomina, O., Stocker, T.F., Tarasov, P., Wagner, M., Widmann, M., 2008. Mid- to Late Holocene climate change: an overview. *Quat. Sci. Rev.* 27, 1791–1828.
- Wille, M., Hooghiemstra, H., Van Geel, B., Behling, H., Jong, A., Van der Borg, K., 2003. Submillennium-scale migrations of the rainforest–savanna boundary in Colombia: ¹⁴C wiggle-matching and pollen analysis of the core Las Margaritas. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 193, 201–223.
- Wolin, J.A., Stone, J.R., 2010. Diatoms as indicators of water-level change in freshwater lakes. In: Smol, J.P., Stoermer, E.F. (Eds.), *The Diatoms: Applications for the Environmental and Earth Sciences*. Cambridge University Press, Cambridge, pp. 174–185.