

POLLEN AND MICROALGAE IN SEDIMENTS AT SOUTHERN
MARGIN OF COLHUE HUAPI LAKE, CHUBUT, ARGENTINA.
AN INSIGHT TO AMONG SHORE COMPARISON

ANÁLISIS DE POLEN Y MICROALGAS EN SEDIMENTOS DE LA MÁRGEN SUR DEL LAGO
COLHUE HUAPI, CHUBUT, ARGENTINA. UNA COMPARACIÓN ENTRE ORILLAS

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RESUMEN

Con el objetivo de conocer las comunidades vegetales del lago Colhue Huapi e inferir los cambios en el nivel del lago ocurridos durante el Holoceno Tardío, se analizó el contenido polínico y algal de un perfil de la margen sur, sitio La Campanita (45°38' S, 68°37' O). El segmento analizado posee dos dataciones ¹⁴C (AMS), una de 1711 ± 35 ¹⁴C años AP a 95 cm de profundidad, correspondiente a la base del perfil, y otra de 979 ± 42 ¹⁴C años AP a 40 cm. Se observó un predominio de taxa no arbóreos, de los cuales Chenopodiaceae fue el taxón arbustivo más importante y Cyperaceae el taxón herbáceo principal. El perfil mostró cambios a nivel local y pocas diferencias respecto del ingreso de polen regional y extra regional. Desde 1711 ± 35 ¹⁴C años AP hasta ca. 1212 años AP, la baja representación de Cyperaceae - relacionada con una menor disponibilidad de sitios someros para colonizar - y los mayores porcentajes de las algas planctónicas estudiadas, sugieren un nivel alto del lago. Entre ca. 1212 y 414 años AP se observa un período de cambio en el nivel del lago, con reiteradas fluctuaciones. La tendencia se modificaría hacia 979 ± 42 ¹⁴C años AP con una disminución del nivel del agua indicado por una expansión de las Cyperaceae y una reducción de las algas. Desde ca. 414 años AP hasta ca. 195 años AP continuó el descenso del nivel del lago aunque con una tendencia más neta y menos fluctuante, indicado por los mayores porcentajes de Cyperaceae del perfil y más bajos para las algas. Para los últimos ca. 195 años AP se registró una recuperación del nivel del lago dada por una reducción de los porcentajes de Cyperaceae, y un leve aumento de las algas. Asimismo, el perfil La Campanita se comparó estadísticamente con un

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perfil extraído de la margen noroeste del mismo lago. Ambas secuencias reflejaron tendencias similares de variaciones de nivel del lago para los intervalos anteriores a 979 ± 42 ^{14}C años AP.

Palabras clave: Polen, PNP, Holoceno, Lago Colhue Huapi, nivel del lago, comparación entre orillas

ABSTRACT

A soil profile from the southern margin of Colhue Huapi Lake, at La Campanita site ($45^{\circ}38'$ S, $68^{\circ}37'$ W), was analysed for pollen and algae content to know the past vegetation communities and to infer changes in lake water level occurred during the Late Holocene. Samples were dated by AMS ^{14}C methods. Radiocarbon ages were of 1711 ± 35 ^{14}C yr BP at the base, 95cm depth, and another of 979 ± 42 ^{14}C yr BP at 40cm depth. The record was dominated by no arboreal taxa, Chenopodiaceae being the principal shrub taxon and Cyperaceae the herbaceous one. Changes in the pollen record occurred mainly at a local scale and few differences were observed in the input of regional and extra regional pollen. From 1711 ± 35 ^{14}C yr BP until ca. 1212 yr BP, a high lake water level was indicated by the low representation of Cyperaceae associated with few shallow areas available to be colonized and high percentages of *Pediastrum* and *Botryococcus* algae. Between ca. 1212 and 414 yr BP a period of changes with several fluctuations in water depth developed. This trend would modify at 979 ± 42 ^{14}C yr BP with a decrease in the waters reflected by the expansion of Cyperaceae and algal reduction. From ca. 414 yr BP until 195 yr BP lake water level continued falling with a less fluctuating and net trend as indicated by the highest percentage of Cyperaceae in the sequence and a low algal representation. The subsequent reduction in Cyperaceae percentage and the moderate increase in the algae would indicate a recovery of the lake water level for the last ca. 195 yr BP. Additionally La Campanita sequence was statistically compared with a sequence obtained from the north-western margin of the lake. Both sites registered a similar trend before 979 ± 42 ^{14}C yr BP.

Key words: Pollen, NPP, Holocene, Colhue Huapi Lake, lake water level, shore comparison.

INTRODUCTION

Lakes represent excellent continental climate archives since their deposits usually span over long periods of time and yield moderately high-resolution paleoenvironmental records (Fritz, 2005). Such sites offer simple continuous sedimentation, dominated by deposits of dead planktonic material that incorporate other particles, such as pollen and spores that are blown or washed into the lake (Bennett & Willis, 2003).

Pollen analysis is an important method for the reconstruction of past vegetation by means of the pollen grains it produced (Faegri & Iversen, 1989). Such reconstructions tend to incorporate other microfossils (Danielsen, 2010) of different origins that are often preserved in pollen preparations. These extra fossils, known as NPP (non-pollen palynomorphs) include remains of algae, cyanobacteria, spores of fungi and

invertebrates, and increase paleoenvironmental information obtained from the samples (van Geel, 2003).

Patagonia is an important source of terrestrial paleoclimate data from the higher southern mid-latitudes as it is the southernmost continental landmass in the southern hemisphere, except for Antarctica (Fey *et al.* 2009). However, well dated high resolution climate archives in southern South America and especially in Patagonia steppe are still scarce (Haberzettl *et al.* 2005; Wille *et al.* 2007; Kilian & Lamy, 2012).

Some paleoenvironmental researchs developed on lentic environments of Patagonia, at Santa Cruz province, include Cardiel Lake (Stine & Stine, 1990; Markgraf *et al.* 2003), Laguna Potrok Aike (Haberzettl *et al.* 2005; Wille *et al.* 2007), Laguna Azul (Mayr *et al.* 2005) and Laguna Las Vizcachas (Fey *et al.* 2009) and incorporate diverse indicators such as pollen, microalgae,

ostracods and stable isotopes.

In this way and taking into account that lake water level oscillation in closed basins is a good indicator of climatic variations (Stockton 1990, Mason *et al.* 1994), different approaches are taking place, in Colhue Huapi Lake, at Chubut province, to know past environments of central Patagonia. Previous researches include identification of prehistoric settlement sites in Colhue Huapi margins belonging to late hunter-gatherers (Arrigoni, 2001)¹ and two palynological studies, one at Alero del Cañadón de las Manos Pintadas (Burry & D'Antoni, 2001) located 50km West of the lake and the other on the north-western margin (Trivi & Burry, 2007).

The aims of this study were a) to infer, through different palynomorphs (pollen and *Pediastrum* and *Botryococcus* algae), changes in vegetation and in Colhue Huapi Lake morphology during the Late Holocene, and b) to analyze the dynamics of the lake through the comparison of profiles from different shores.

Study Area

Colhue Huapi Lake is located at the southern area of Chubut province (45°30' S, 68°45' W and 258 m asl) in the geomorphological region called Extra-Andean Patagonia (Fig. 1). Together with Musters Lake, they represent the greatest natural lentic environments along this region (Paruolo *et al.* 1998). Senguer River is the only influent of the system and its headwaters are located in the Andes mountain, in Fontana and La Plata Lakes (Fig. 1) (Calcagno *et al.* 1995; Montagna, 2007²). The main course of Senguer River divides before entering Musters Lake and contributes to Colhue Huapi Lake through an arm called Falso Senguer (Montagna 2007)². From the south-eastern margin of Colhue Huapi Lake emerges the only effluent, Chico River, a temporary watercourse that flows into the Chubut River (Coronato & del Valle, 1988).

Colhue Huapi is a shallow water body with a mean depth of 2m and a surface area of 810km² (Quirós, 1988)³. It is a high irregular basin with a shoreline development (D) of 2.181 according to Dangavs equation (1995). A value of 1 for shoreline development is expected in lakes with circular morphometry and a larger value indicates that the shoreline is highly dissected (Dodds & Whiles, 2010).

Colhue Huapi occupies a large shallow depression of structural and eolic origins. The deepest zones are located northward and near the Península Grande whereas the shallowest areas are in the southern area, in the vicinity of the outflow stream (Fig. 1) (Rivas, 1978)⁴. Oral records and satellite studies evidence the lake has undergone marked fluctuations in its morphology and water level in the last years (Coronato, 2003). Due to the shallowness of this waterbody, changes on the hydrologic budget originate big fluctuations in the basin area (Coronato, 2003; Tejedo, 2003⁵).

The Lake is situated in an arid zone of Argentina with a mean annual precipitation of 150mm and temperature of 10.9°C (Quirós *et al.* 1983). Winds from the West feature Patagonian climate and are characterized not only by their persistence during the year but also by their intensity and low humidity content (Paruolo *et al.* 1998). West to East decrease in precipitations in southern Chubut leads to a vegetation gradient from forest to different grass and shrub steppes (León *et al.* 1998).

Colhue Huapi belongs to the Chubutense subdistrict of the Patagonian phytogeographic province (Soriano, 1956). This subdistrict is characterized by a shrub steppe composed of desert and semi desert vegetation. Plants are adapted to drought and wind, and shrub species usually have spines and their leaves are reduced.

In plains above 400 m asl vegetation is dominated by shrubs such as *Chuquiraga avellanadae* Lorentz 1881, *Nassauvia glomerulosa*

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3 Quirós, R. 1988. Mapas batimétricos y parámetros morfométricos de lagos patagónicos del Neuquén, de Río

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4 Rivas, A. 1978. Batimetría del lago Colhue Huapi. CENPAT Centro Nacional Patagónico, Contribución N°18: 1-8.

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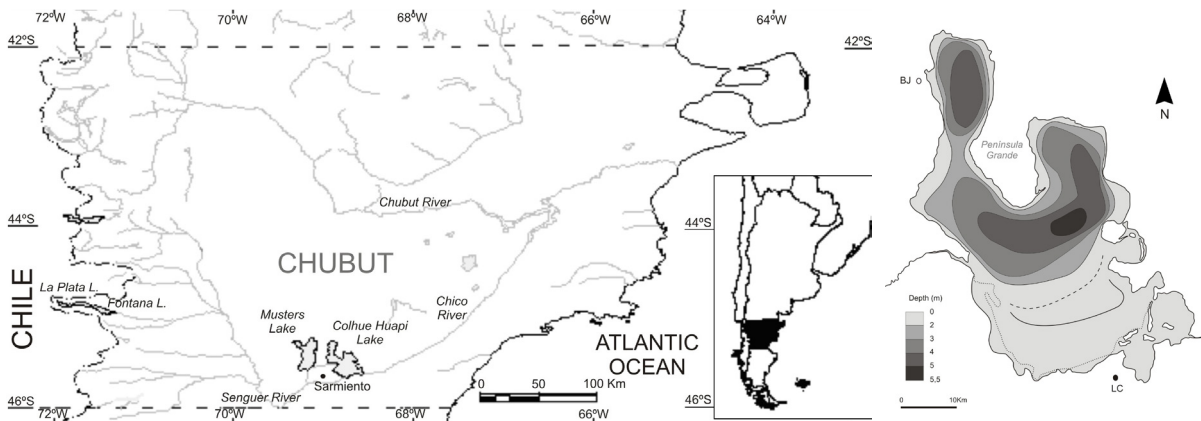


Fig. 1. Location of Colhue Huapi Lake, lake' bathymetry (modified from Rivas 1978)4. LC: La Campanita, BJ: Boliche de Jerez sites.

(Lindl.) D. Don 1832 and grass species as *Stipa chrysophylla* É.Desv. 1854, *S. humilis* Brot. 1804, *S. speciosa* Trin. & Rupr. 1842 and *Poa ligularis* Nees ex Steud. 1854. In depressed areas halophyte species as *Frankenia patagonica* Speg. 1897, *Lycium ameghinoi* Speg. 1897, *Prosopis denudans* Benth. 1841 and the Chenopodiaceae *Atriplex lampa* (Moq.) D. Dietr. 1852 and *Atriplex sagittifolia* Speg. 1897 thrive. South of Colhue Huapi and Musters Lakes, halophyte vegetation alternates with *Chuquiraga avellanadae* and *Nassauvia glomerulosa* communities (Soriano, 1956; Paruelo *et al.* 1992). Senguier River originates a wide depositional plane entering the lakes covered by mallines. Moreover, periodically flooded places are usually covered by lawn of *Juncus lesueurii* Bol. 1863 and Poaceae such as *Distichlis scoparia* (Kunth) 1897 and *D. spicata* (L.) Greene 1887, which grow in brackish soils (Soriano, 1956; Correa, 1978).

MATERIALS AND METHODS

Twenty sediment samples were collected every 5 cm in a profile at the southern margin of Colhue Huapi Lake, in La Campanita site (45°38'S – 68°37'W) (Fig. 1). Two samples (14 and 18) were later divided in the laboratory in the subsamples inferior (i) and superior (s).

The extraction of pollen from sediments was performed according to Faegri & Iversen standard procedures (1989). Three tablets of *Lycopodium clavatum* L. (1753) spores were

added to each sample for a reassurance that no part of the sample has been lost during the extraction process. Subsequently, samples were sieved through a 260µm mesh. The material was deflocculated and humic acids were neutralized with potassium hydroxide. Chloride acid was added to remove carbonates. Organic and inorganic compounds were separated by differential flotation in a ZnCl solution ($\delta=1.9\text{g/l}$). Silicates were then removed with hydrogen fluoride (HF) and cellulose by acetolysis. Finally, residues were included in glycerine and transferred to 5ml vials.

Pollen was counted on microscope with 400x to 1000x magnification. Identifications were based on published atlases (Heusser, 1971; Markgraf & D'Antoni, 1978; Moore *et al.* 1991) and on comparisons with a reference collection from the Palynology Laboratory (Universidad Nacional de Mar del Plata). Determination was done to class, family or genus level according to the resolution degree achieved at microscope. Samples were counted to a pollen sum of 300 grains excluding Cyperaceae and Monocotyledoneae (except Poaceae). *Azolla* and algae were also excluded from pollen sum. Percentages of *Azolla* and algae were based on total palynomorph sum including pollen, spores and algae. Statistical analysis was performed with taxa having more than 2% of total pollen sum in at least one sample. Constrained Cluster analysis was processed using the Orloci Distance (TGView 2.02, Grimm, 2004) and Ordination by correspondence analysis of Tilia pack, 1.12 version (Grimm, 1992).

Table 1. AMS radiocarbon dates from core La Campanita of Colhue Huapi Lake.

Sample	Depth (m)	Radiocarbon age (¹⁴ C years BP)	Calibrated age (cal yr BP)	Dated material	Lab no.
1	0.95	1711 ± 35	1484 – 1630	Organic	AA69389
12	0.40	979 ± 42	760 – 927	Organic	AA69390

Additionally, a constrained Cluster analysis, using the Euclidean Distance, was performed with NPPs and pollen of the aquatic taxa (*Azolla* sp., Cyperaceae, Monocotyledoneae, *Myriophyllum* sp. and *Triglochin* sp.) to assess the dynamics of the aquatic communities. Finally, La Campanita sequence (LC) was compared with the Boliche de Jerez (BJ) profile (Trivi & Burry, 2007), obtained from the north-western margin of Colhue Huapi Lake, to analyze the dynamics of the water body. Taxa in common and having more than 2% of representation in at least one sample were used in the statistical analysis. Given that NPPs of BJ were not quantified but expressed in a qualitative scale (absent, poor and frequent), only pollen taxa were considered in the among sites comparison. LC and BJ samples were analyzed together by Cluster analysis without stratigraphic restriction and by Detrended Correspondence Analysis (DCA). Subsequently, LC and BJ scores of the first axis of common DCA were plotted against

time to visualize the changes in the lake water level.

Profile description

La Campanita profile was divided in three lithological units as follows: a basal section having fine, homogeneous and wet sediment (100-60cm depth), a middle unit of rectangular and compact blocks with roots (60-10cm depth) and an upper section characterized by the presence of small blocks with a great density of roots and giant bulrush (*Schoenoplectus californicus* (C.A.Mey.) Soják 1972) macro-remains (10-0cm depth) (Fig. 2).

Radiocarbon ages of two samples were determined by AMS ¹⁴C dating techniques at the Laboratory of Isotope Geochemistry of Arizona University (Table 1). Radiocarbon ages were then calibrated with the software Calib 5.1 Beta and corrected for the southern hemisphere, 2 sigma (Stuiver & Reimer 1993). Chronology according to samples' depth was calculated with Tilia 1.7.15.

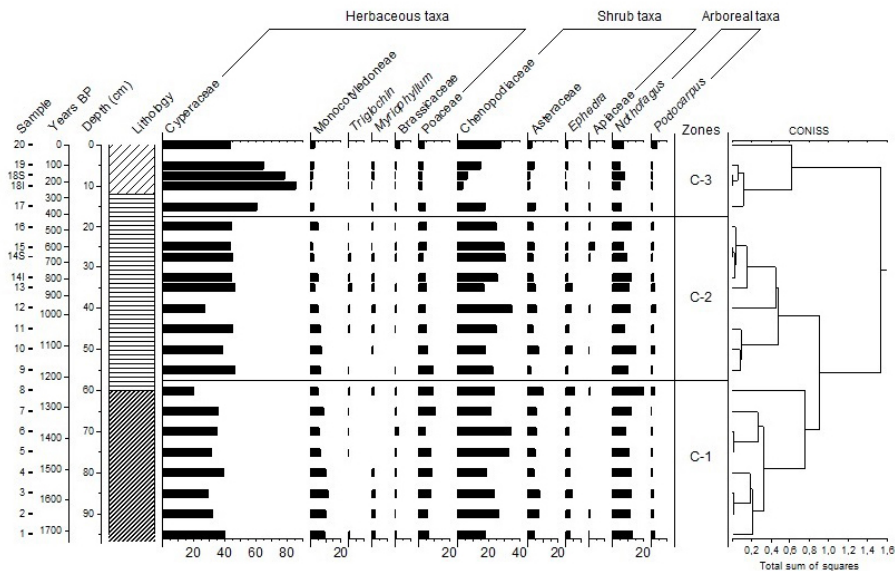


Fig. 2. Pollen diagram of taxa > 2%. Samples, chronology, depth, lithology and pollen zones according to constrained cluster analysis are indicated. i: inferior, s: superior

Sedimentation rate determined by depth and radiocarbon dates was of 0.075 cm yr⁻¹ before 979 ± 42 ¹⁴C yr BP and of 0.041 cm yr⁻¹ after that date.

RESULTS

In this study 21 pollen types, microspores of the free floating pteridophyte *Azolla* sp. and two non-pollen palynomorphs (NPPs) corresponding to the algal genera, *Pediastrum* and *Botryococcus*, were determined.

The pollen record was dominated by non-arboreal elements, including seven herbaceous and 11 shrub ones (Fig. 2).

Cyperaceae, Monocotyledoneae and Poaceae were dominant among herbaceous taxa and Chenopodiaceae among shrub ones. As well, three extra regional taxa from the eastern fringe of subantarctic forest *Podocarpus*, *Nothofagus* and *Misodendron*, a parasite of the latter, were found.

Constrained cluster analysis divided the profile in three zones (Fig. 2). From bottom to top the different units are characterized as follows:

C-1 (95 – 57.5 cm): grouped samples 1 to 8, from 1711 ± 35 ¹⁴C to ca. 1212 yr BP. This section was dominated by Cyperaceae (20-40%) and Chenopodiaceae (18-34%), and included the greatest percentages of Monocotyledoneae (5-11%), Poaceae (5-11%), Asteraceae (4-10%), *Ephedra* sp. (2-6%) and the arboreal taxon *Nothofagus* (8-20%).

C-2 (57.5 – 17.5 cm): samples 9 to 16, from ca. 1212 to 414 yr BP. In this zone Cyperaceae and Chenopodiaceae still remained the dominant taxa. Chenopodiaceae ranged from 17 to 35%, Monocotyledoneae (1-7%), Poaceae (2.5-9%) and Asteraceae (<7%) percentages declined from the previous zone.

Ephedra sp. declined compared to the underlying zone and from samples 14i to 16 the percentages were slightly lower (1-2%) and constants.

Among arboreal taxa, *Nothofagus* oscillated between 7 and 15% whereas *Podocarpus* values were low and moderately constant at the top of the zone (samples 14i to 16).

The aquatic taxa *Triglochin* and

Myriophyllum reached high values towards the middle of this unit.

C-3 (17.5 – 0 cm): 17 to 20 samples included the latest ca. 414 yr BP. Cyperaceae dominated this zone and reached the maximum percentages for the entire record, whereas Chenopodiaceae decreased and showed the lowest ones. Monocotyledoneae, *Myriophyllum*, Poaceae, Asteraceae and *Ephedra* decreased as well.

Arboreal taxa were poorly represented in this zone, except for *Podocarpus* at the surface sample.

The surface sample markedly differed from the others of the same zone. This sample was characterized by the lowest percentages of Cyperaceae (44%) and the highest values of Chenopodiaceae (28%), Monocotyledoneae (3%), Brassicaceae (3%) and *Podocarpus* (4%), while the aquatic genus *Myriophyllum* was not represented.

Ordination of pollen samples by means of correspondence analysis explained 63% of the variance with the first axis and 20% with the second axis (Fig. 3-a). Samples were mainly arranged according to the cluster analysis of Fig. 2.

Samples belonging to zone C-1 and sample 10 from C-2, were grouped near the right edge of axis 1 and the bottom of axis 2. Accordingly, the variables explaining this ordination were *Ephedra*, Asteraceae and Chenopodiaceae, among shrub taxa; Monocotyledoneae and Poaceae, among herbaceous taxa and *Podocarpus* sp. and *Nothofagus* sp., among arboreal taxa (Fig. 3-b).

The remaining samples of C-2 and sample 20 were located at the middle of the first axis and more scattered along the second axis. Chenopodiaceae, Brassicaceae, *Nothofagus* sp. and the aquatic genera *Myriophyllum* and *Triglochin* explained the ordination of these samples (Fig. 3-b).

Finally, samples of C-3 stayed in the left edge of the first axis and Cyperaceae was the main variable determining this group (Fig. 3-b).

Analysis of non-pollen palynomorphs and other aquatic taxa

The constrained cluster analysis of the communities of aquatic vegetation divided the record in two zones (Fig. 4):

Zone 1 (95 – 33.5 cm): grouped 1 to 13

samples from 1711 ± 35 ^{14}C yr BP to ca. 822 yr BP. This unit was dominated by *Pediastrum* sp. (40-70%) and in a lesser extent by *Botryococcus* sp. (<8%).

Cyperaceae (20-47%) was dominant among aquatic plants, Monocotyledoneae, *Triglochin* sp.

and *Myriophyllum* sp. were present in a lower proportion.

Zone 2 (33.5 – 0 cm): includes 14i to 20 samples, from ca. 822 yr BP to the present. This zone showed decreased contribution of algae with respect to total palynomorphs and increased

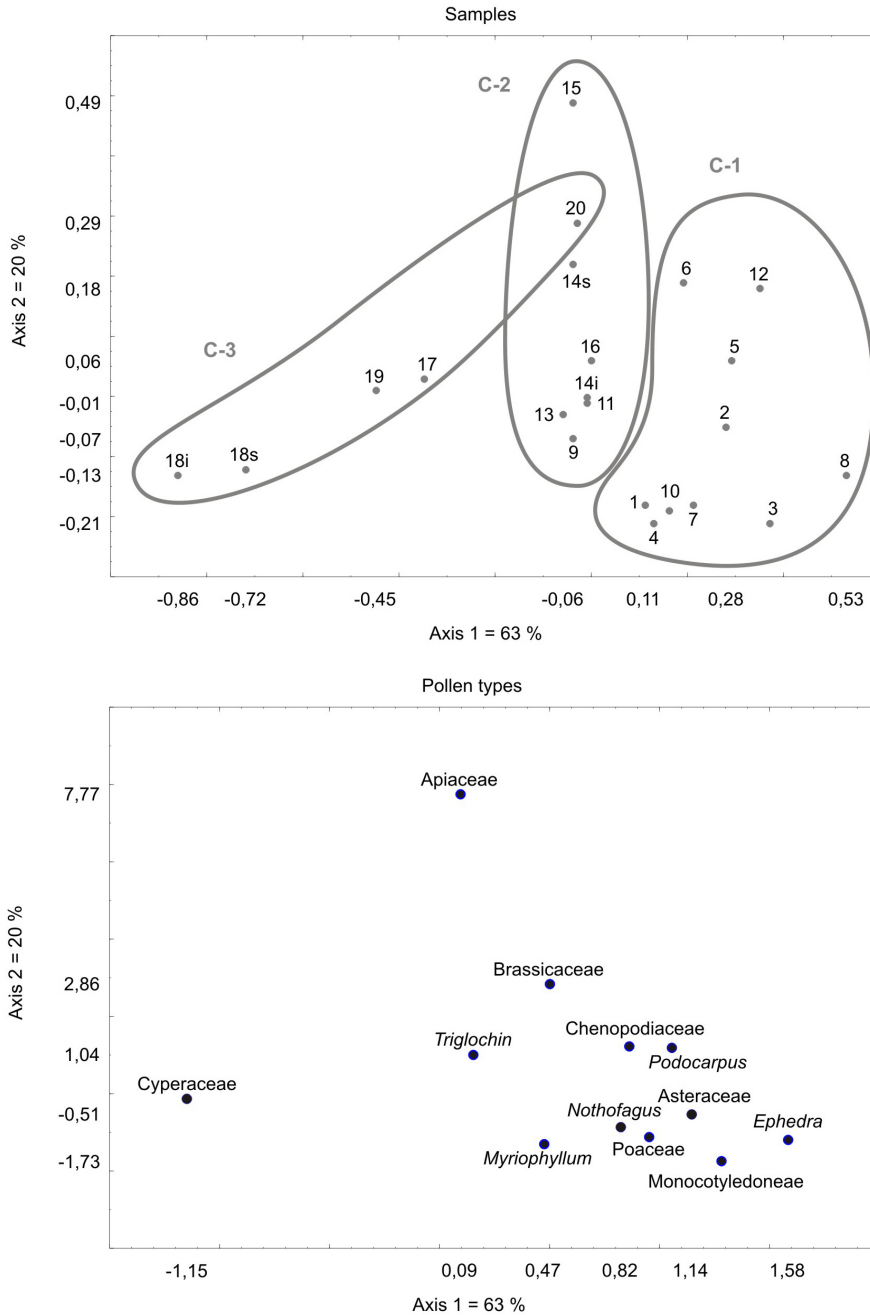


Fig. 3. First two axis of Correspondence analysis. a) Samples scores. b) Pollen variable scores. i: inferior, s: superior.

representation of aquatic plants, mainly Cyperaceae (44-86%) and *Azolla* sp. (<7%). The other aquatic taxa were poorly represented.

Comparison with Boliche de Jerez (BJ) profile

La Campanita pollen spectrum (LC) was compared with Boliche de Jerez pollen assemblage (BJ) studied by Trivi & Burry (2007) (Fig. 5). In both sequences non arboreal taxa predominated. LC and BJ shared seven pollen types though the contribution of some of them (herbaceous taxa Monocotyledoneae and Poaceae) was higher at BJ. On the other hand, Chenopodiaceae (a shrub taxon) was higher at LC. Those differences were also found in surface samples (LC20 and BJ13).

A common cluster analysis of LC and BJ delimited five groups (Fig. 5). Only one of these included samples of both sites. Both spectra were grouped separately and in the same way as in individual analyses.

The ordination of pollen samples along first axis of DCA of both profiles versus time

was performed in order to visualize, through the response of both sites, the changes in lake water level experienced at both margins. LC and BJ samples arranged separately (Fig. 6). The irregularity of the curve suggests rapid environmental shifts with changes among wet and dry phases. Before ca. 1000 yr BP both sites shared a trend at similar timescales but they were to some extent out-of-phase. From bottom to top the first increase along axis 1, was recorded earlier at LC3 than at BJ. Afterwards, both profiles showed an almost simultaneous decline at LC6 and BJ4 (Fig.6).

DISCUSSION

Pollen rain can be divided into different components according to the distance from its source. From further to nearer pollen is classified as extra-regional, regional, extra-local and local (Janssen, 1966). La Campanita pollen can be analysed through those elements. Arboreal taxa could not be attributed to the nearby vegetation of Colhue Huapi Lake; instead they are an example of

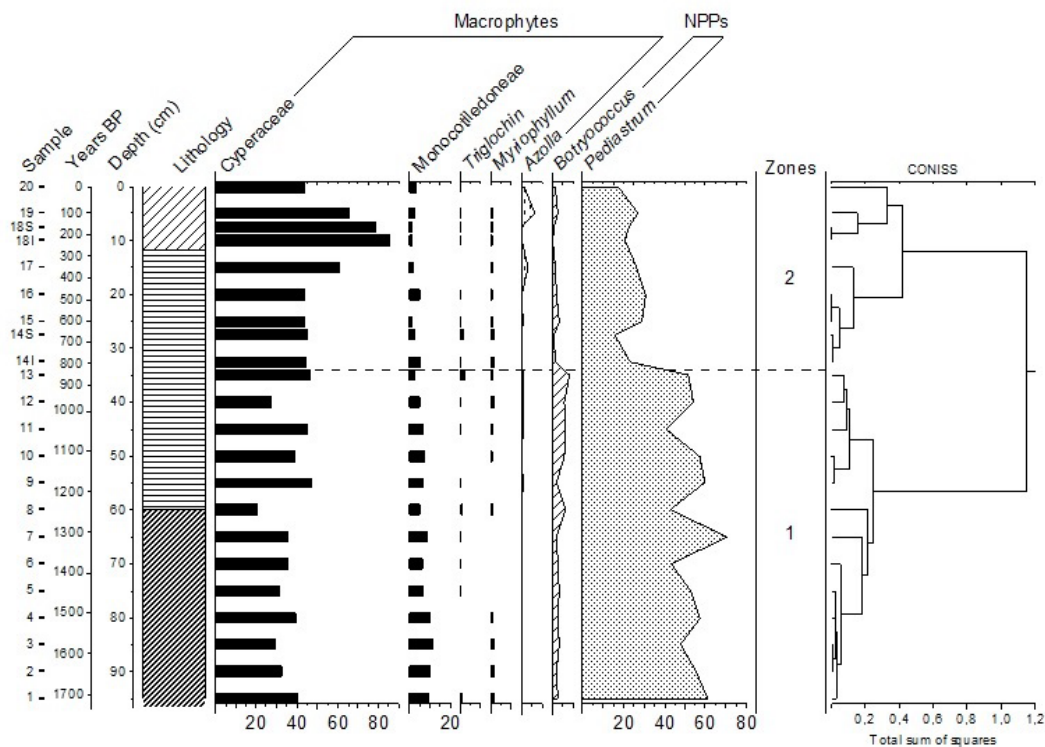


Fig.4. Pollen diagram of aquatic taxa and NPPs. Sample, chronology, depth, lithology and pollen zones according to constrained cluster analysis are indicated. i: inferior, s: superior. NPPs: Non-pollen Palynomorphs.

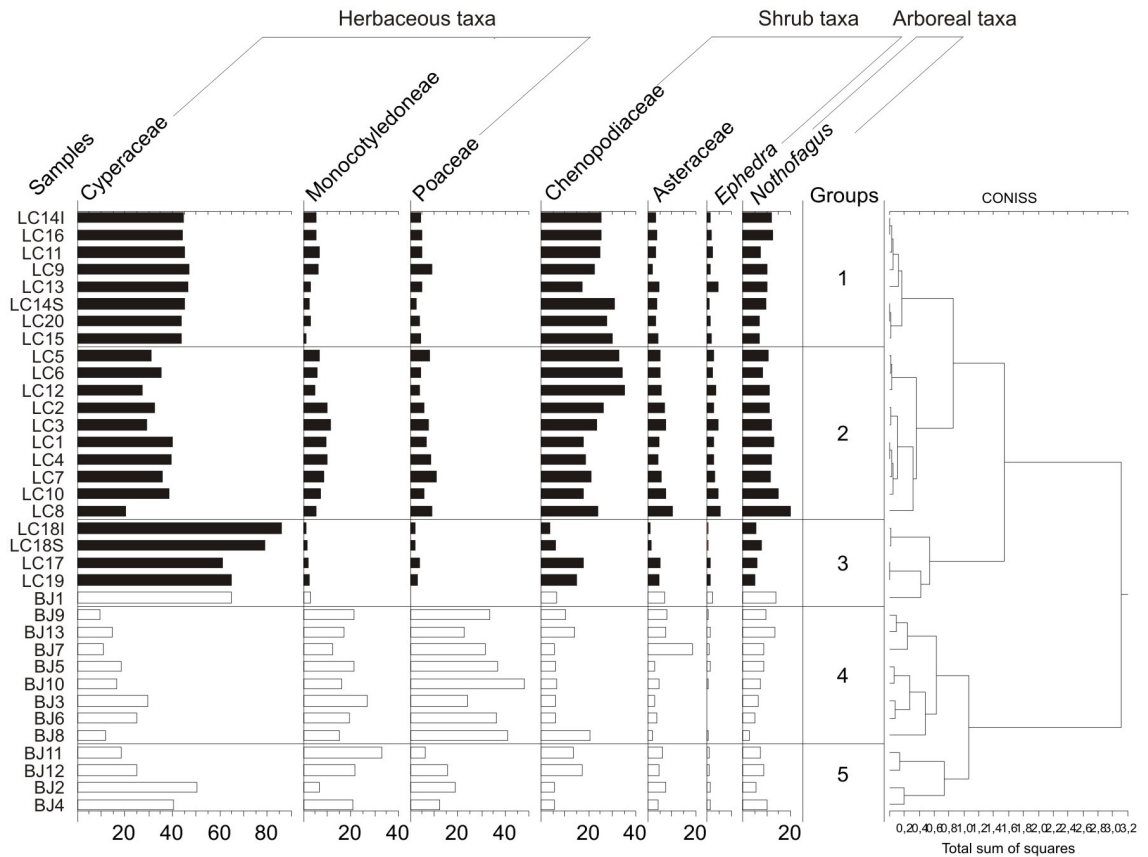


Fig.5. Groups defined by the unconstrained cluster analysis of La Campanita (LC, black bars) and Boliche de Jerez (BJ, white bars) samples. i: inferior, s: superior.

extra regional pollen coming from the subantarctic forest on the west. The preponderance of *Nothofagus* species, in the forest, was also detected in the pollen spectrum as its pollen predominated among arboreal taxa throughout the record. Its presence might be due to air transport by constant winds from the west and by water transport through Senguer River input since La Plata and Fontana lakes basins are covered by *Nothofagus* trees (Calcagno *et al.* 1995, Modenutti *et al.* 1998). Today *Podocarpus* species occur mainly in occidental slopes of Los Andes, mostly in the Chilean side, and the distribution ranges southward 40 °S (Donoso & Utreras, 2007; Donoso *et al.* 2007). Thus the observed contribution to the pollen assemblage might be due to the influence of constant winds from the west. In agreement with La Campanita, other records of extra Andean Patagonia also show input of Andean forest

elements (Markgraf *et al.* 2003; Wille *et al.* 2007).

On the other hand, non arboreal taxa, that dominated the whole record, represent the local and regional elements. Poaceae pollen might belong to the halophyte species *Distichlis scoparia* and *D. spicata* that thrive on desiccated shore areas around these water bodies. Thus it can be considered a local component.

Chenopodiaceae are another halophyte taxa. At present in Colhue Huapi, *Atriplex lampa* and *A. sagithifolium* grow at Sarmiento basin and in the south of the lakes where the extensive evaporation of water originates large salt areas (Iglesias de Cuellos, 1982; Correa, 1984). As Chenopodiaceae representation decline rapidly with distance to the source (Markgraf *et al.* 2003), the abundant Chenopodiaceae pollen found at La Campanita was attributed to those species and is considered a local component too.

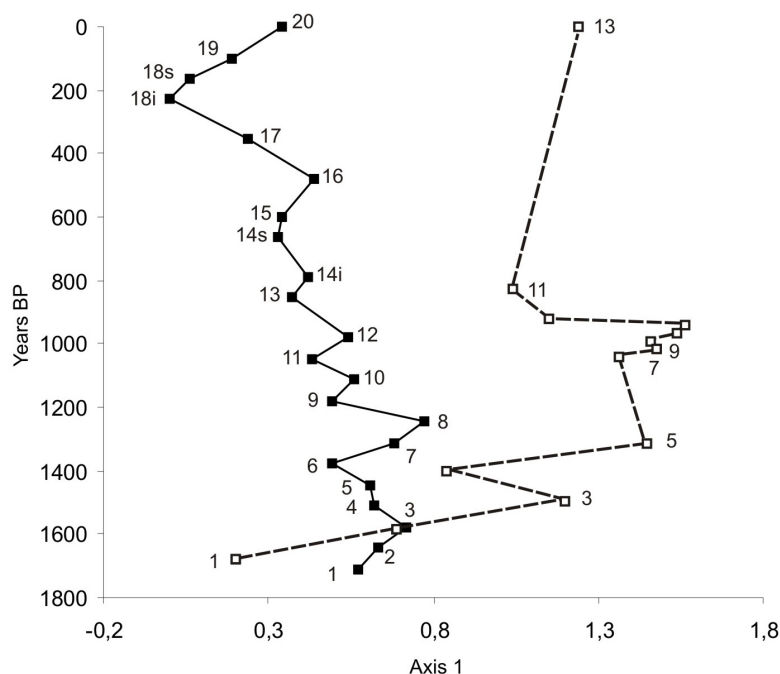


Fig. 6. First axis of DCA of La Campanita (solid line and dark squares) and Boliche de Jerez (dashed line and open squares) samples vs. time. i: inferior, s: superior.

Cyperaceae, *Triglochin* and *Myriophyllum* are hydrophytes; thus they would represent autochthonous pollen of the lake.

The remaining non arboreal taxa might belong to regional pollen of the steppe. This regional pollen was the richest one compared to the other components even though the individual representation was low, with most taxa under 2%. Shrubs represent the principal cover of the steppe (de la Vega, 2010).

In the Patagonian steppe there are three functional groups that responds in a similar manner to perturbations such as intense droughts. These are: coirones (short and compact perennial grasses), shrubs and herbs. Usually, herbs endure more intense drought conditions than shrubs (de la Vega, 2010; Golluscio *et al.* 2011).

Two local taxa, Cyperaceae and Chenopodiaceae, clearly dominated the pollen spectrum. One reason of this greater representation of local pollen respect to the regional one, might be the different pollen production and dispersal. For instance, the dominant species of the region, the Asteraceae *Nassauvia glomerulosa* and *Chuquiraga avellanadae*, are zoophilous

plants and so have a small pollen production and liberation. Instead, Cyperaceae and Chenopodiaceae are wind pollinated plants and abundant pollen producers (de la Vega, 2010). Another reason might be the location of the sampling site. Other studies developed at Extra-Andean Patagonia's lakes (Markgraf *et al.* 2003; Trivi & Burry, 2007) present a similar pattern. At low lying places, such as lacustrine environments of arid regions, the regional picture can be masked by pollen produced locally (Horowitz, 1992). Not only higher percentages of wind pollinated plants but also greater abundances of plants that contribute minimal amounts of pollen to the pollen rain. In this way regional elements might be recognizable not in percentages but in number of taxa.

In terms of water level, increased input of pollen of local halophytes might suggest an expansion of desiccated areas close to the shore during a period with low lake level (Mayr *et al.* 2005).

On the other hand, Cyperaceae usually indicates the presence of wet habitats in peat bogs (Mancini, 1998; 2009) or in lakes (Whitlock *et al.* 2006). Laine *et al.* (2010) associated the increase

in Cyperaceae to a reduction of the water level of the pond. As La Campanita site is located at the shallowest zone of the lake, we also associated increased Cyperaceae input to a drier situation. Littoral helophytes can expand towards the middle of the wetland when low water level originates more extensive shallow water areas (Rossi & Tur, 1976; Coops *et al.* 2003; Mayr *et al.* 2005).

The *Pediastrum* remains found in surface samples at La Campanita might not only be an example of the resistance of this algae cell wall (Weckström *et al.* 2010) but also it might be an evidence of a previously under water place. As instance, some years after Footprint Lake in Alaska was artificially drained, sediments were still rich in *Pediastrum* colonies (Livingstone *et al.* 1958). In agreement to this, oral evidence suggests that LC site had been under water in the 60's (Juan Vera *personal communication*).

At present *Pediastrum* colonies occur predominantly in the plankton in temperate eutrophic lakes, whereas in oligotrophic lakes *Pediastrum* taxa are often confined to the littoral zone associated to aquatic macrophytes (Weckström *et al.* 2010). Many algae, including *Pediastrum*, persist in littoral macrophytes when multiplication rates in free water reduce and cannot compensate the lost (Margalef, 1983). As littoral macrophytes stabilise bottom and enhance sediment accumulation (Dearing, 1997), a positive correlation between Cyperaceae and algae would be expected. However, this is not supported by La Campanita data.

Several paleoecological studies relate increase in *Pediastrum* with decreasing water depth (Markgraf *et al.* 2003; Whitlock *et al.* 2006), while others associate the decline of this algae with decreasing water level (Laine *et al.* 2010). Fey *et al.* (2009) found a positive correlation between abundance of littoral vegetation and epiphytic diatoms. In addition, the highest percentages of epiphytic taxa occurred at the expense of the planktonic ones. At La Campanita we found a negative correlation between littoral vegetation and *Pediastrum* and *Botryococcus* planktonic algal genera. Higher percentages of Cyperaceae occurred when algae values were low. At present a similar trend is found in the two alternative states of shallow lakes. In which the clear state is dominated

by aquatic vegetation and has low algal biomass, and the turbid one is characterized by high algal biomass and poor aquatic vegetation (Scheffer *et al.* 1993). Furthermore an important factor for the switch between those alternative equilibria is the change in the water level (Scheffer *et al.* 1993).

The main change in *Pediastrum* sp. and *Botryococcus* sp. observed at LC from ca. 979 ± 42 ^{14}C yr BP, was probably due to a bigger alteration in lake conditions than the ones observed in the algae before and after that time. This change, such as a low lake level, also triggered the expansion of Cyperaceae. Consequently if it is so, the Colhue Huapi Lake could have switched from a turbid to a clear state around 979 ± 42 yr BP (Fabiani *et al.* 2009).

The present reconstruction of Colhue Huapi, based on the cluster and ordination analyses, suggests that the lake went through several water level fluctuations during the timescale analysed. From 1711 ± 35 ^{14}C yr BP to ca. 1212 yr BP low percentages of Cyperaceae related with few shallow habitats available for colonization and high values of the algae studied might suggest high lake water level.

Water levels higher than today are testified by archaeological remains found near La Campanita and dating ca. 1500 yr BP and ca. 1250 yr BP. Arrigoni (2001)¹ proposed that those places have been the bottom of the lake during the highest lake water level. In agreement with Arrigoni (2001)¹, pollen samples for those dates indicate high water level.

Between ca. 1212 and 414 yr BP a period of changes with several water level fluctuations developed, as shown by the changes in Cyperaceae until ca. 979 ^{14}C yr BP. This trend would modify at ca. 979 ^{14}C yr BP with a higher constancy in Cyperaceae values. Cyperaceae could expand to newer shallow regions and the decrease in algae might reflect a reduction in water level. From ca. 414 yr BP to 195 yr BP lake level would have continued to decrease with a less fluctuating and net trend as indicated by the highest percentages of Cyperaceae of the sequence and low of the algae. The increase in *Azolla* percentages after ca. 414 yr BP would agree with a low lake water level since this free floating pteridophyte grows in environments with still waters and reduced flow

(Carrapiço, 2001).

At present, the sampling site LC is dried up, but according to oral evidence around the second half of XX century the lake registered higher levels than today. The less fluctuating trend found in La Campanita from ca. 195 yr BP is not supported by historical nor oral records which indicate that repeated fluctuations of Colhue Huapi Lake have occurred since 1800 (Arrigoni, 2001⁵; Coronato, 2003, Juan Vera *personal communication*). Due perhaps to a low resolution of the profile, the short term variations in water level observed in the last years were not registered. As instance, a huge reduction of water level occurred in 2000 and five years later the lake had recovered (Tejedo, 2003⁵; Casal *et al.* 2007). Part of those changes might be due to human impact. During dry seasons, the connection between Musters and Colhue Huapi Lakes is cut off, reducing the flow towards the later (Coronato, 2003; Tejedo, 2003⁵; Secr. Recursos Hídricos Nación, 2007⁶).

Other lakes of Patagonia showed a recession in the last century (Laguna Potrok Aike, Haberzettl *et al.* 2005). Lago Cardiel instead, after its latest low stand in 1990, has risen approximately 4m (Markgraf *et al.* 2003).

The comparison of LC with the BJ sequences from the north-western margin of the lake showed differences in sedimentation rates. As instance, sediment yielded an age of 979 ± 42 ¹⁴C yr BP at 40cm depth at La Campanita whereas at Boliche de Jerez an age of 920 ± 35 ¹⁴C yr BP was already observed at only 18cm (Trivi & Burry, 2007). This might be explained by a different sedimentation dynamics among margins (Dearing, 1997).

The sampling sites might influence the way changes in lake level are perceived. BJ profile was obtained from the paleo beach located at the west arm of the lake. The depressed areas west and east of Península Grande are due to soft synclines (Sciutto, 2003)⁷.

The LC assemblage is from the southern shore of the lake, where Senguer River enters Sarmiento plain (Bajo de Sarmiento) and originates

a floodplain of more of 200 km² area (Sciutto, 2003)⁷.

Moreover the north-western area of the lake is deeper and presents steep margins whereas the southern zone is shallower and lake level changes are more intensively experienced (Rivas, 1978⁴; Coronato, 2003).

Probably a bigger homogeneity in the records could be expected from sequences obtained from a more regular water body. Given that Colhue Huapi is a highly irregular watershed (with a D=2.181) variations might not be perceived in a uniform manner.

Lake sedimentation processes are complex even in apparently simple basins and the vulnerability of the lakeshore to erosion is varied and would depend on slope profile, soil composition, sediment types and compactness (Dearing, 1997). One difficulty of using near-shore cores is that it is possible that part of the sediment archive may be lacking as a result of reworking of previously deposited sediment or wave action (Dearing, 1997; Laird & Cumming, 2009). Thus the determination of an appropriate site, such as locations with sheltered margins, is a key component in lake-level reconstruction (Dearing, 1997). This might be done if accumulation of near shore sediments is adequate or by defining the dominant sedimentation mechanisms through the study of bathymetric maps as instance (Dearing, 1997; Laird & Cumming, 2009).

When analysing LC and BJ records with others of extra Andean Patagonia, Cardiel Lake (Stine & Stine, 1990; Markgraf *et al.* 2003), Laguna Potrok Aike (Haberzettl *et al.* 2005; Wille *et al.* 2007), Laguna Azul (Mayr *et al.* 2005) and Laguna Las Vizcachas (Fey *et al.* 2009), some inconsistencies appear. Hence some wet and dry periods seem to be out-of-phase and do not reveal a clear trend (Table 2).

Water-level fluctuations are the result of a change in the water budget and, therefore, depend on the amounts of precipitation and evaporation, catchment size and characteristics, and on the

⁵ Tejedo, A. G., 2003. Degradación de suelos en los alrededores del Lago Colhué Huapi, Escalante, provincia de Chubut. Servicio Geológico Minero Argentino-SEGEMAR.

⁶ Secretaría de Recursos Hídricos de la Nación. 2007. Estudio de impacto ambiental, Presa "Los Monos" – Provincia de Chubut.

⁷ Sciutto, J. C. 2003. Curso de Geología de campo: Comodoro Rivadavia – Sierra de San Bernardo. Universidad Nacional de la Patagonia "San Juan Bosco". <http://www.fcen.unp.edu.ar/catedras/sedimentologia/Guiadecampo.pdf>

Table 2. Climatic tendencies at regional scale for the timescale studied in La Campanita profile.

Years BP	Laguna Azul	Laguna Potrok Aike	Laguna Las Vizcachas	Lago Cardiel	Alero de Las Manos Pintadas	Boliche de Jerez	La Campanita
	(52°05'S, 69°35'W)	(51°58'S, 70°23'W)	(50°42'S, 71°59'W)	(48°48'S, 71°13'W)	(45°28'S, 69°42'W)	(45°15'S, 68°53'W)	(45°38'S, 68°37'W)
	Mayr <i>et al.</i> 2005	Haberzettl <i>et al.</i> 2005	Fey <i>et al.</i> 2009	Stine & Stine, 1990; Markgraf <i>et al.</i> 2003	Burry & D'Antoni, 2001	Trivi & Burry, 2007	Present study
-		↓ level		↓ lev. 1940-90 dC			
50	250 - 50 BP						195 BP - present
150	↑ level						
250			300 - 200 BP ↑ T°			920 BP - present	414 - 195 BP
350	600 - 300 BP		500 - 300 BP			↑ level	
450	Dry		↓ T°		1300 BP - present		
550		710 - 540 BP			+ dry		
650		↓ level	850 - 650 BP				979 - 414 BP
750			↑ precipit				
850				lake transgression			
950						1360 - 920 BP	
1050						↓↓ level	1212 - 979 BP
1150						Lowest level	
1250							
1350						1586 - 1360 BP	1711 - 1212 BP
1450				↑ level 1450 BP	1700 - 1300 BP	↓ level	↑ level
1550					+ wet	Before 1586 BP	
1650						↑ level	
1750						Highest level	

discharge conditions (inflow versus outflow) of the basin (Hofmann *et al.* 2008).

They are connected to climatic changes, changes in the large atmospheric pressure systems, or, to seasonal variations and to anthropogenic use of water resources.

In general fluctuations relate to climate in such a way that colder and / or wetter phases are linked with high lake water levels while warmer and/or drier phases with low levels (Shennan, 2005). However basins and catchments having differences in area and volume can differ in the

magnitude and moment of change in response to the same climatic forces (Mason *et al.* 1994). This might explain, in part, the dissimilarities at the beginning of dry and wet periods observed at the paleoreconstructions.

On the other hand, a higher correspondence was found when contrasting with Alero del Cañadón de las Manos Pintadas record (Burry & D'Antoni, 2001), which might probably be due to its proximity. Before *ca.* 1300 ¹⁴C yr BP the wet period correlate, to some extent, with the high stands registered at LC and BJ sites as seen in Table 2. A weaker concordance is found after that date, when the development of a halophyte shrub steppe suggests drier conditions at Alero record and fluctuations are observed in the basin sequences. Present intra- and inter-annual lake level fluctuations of Colhue Huapi are mainly related to the amount of precipitation falling as snow during austral winters in its headwaters in the Andes mountain, while the low level is influenced by human use and by the evaporation rate due to the temperature and drying action of constant winds in the region (Calcagno *et al.* 1995; Coronato & del Valle, 1988; Coronato, 2003).

CONCLUSIONS

The main changes in pollen spectrum at La Campanita site occurred in two local taxa: Cyperaceae and Chenopodiaceae, while few differences were found in the contribution of regional and extra-regional pollen. As a consequence, the sequence would be reflecting changes at a local scale. Lake level fluctuations were associated principally to changes in Cyperaceae and NPPs, *Pediastrum* and *Botryococcus*.

The paleoclimatic inferences indicate that before *ca.* 1212 yr BP lake level was high related to low values of Cyperaceae and the maximum percentages of *Pediastrum* and *Botryococcus* algae. Between *ca.* 1211 and 414 yr BP a period of changing lake water level took place. Until *ca.* 979 ¹⁴C yr BP lake level was high and since then, a decrease would have occurred suggested by an increase in the representation of Cyperaceae and a reduction in algae. From *ca.* 414 yr BP up to 195 yr BP lake water level would have continued its reduction, as indicated by the highest percentages

of Cyperaceae of the sequence and low algal proportion. Finally, for the last *ca.* 195 yr BP, the reduction in Cyperaceae would mark a recover trend of the lake water level.

The pollen and algae record from La Campanita site might contribute to our better understanding of climatic changes and vegetation relation in the Colhue Huapi system. The comparison among sites of different shores provided new insights to the reconstruction and would enhance our comprehension of the dynamics of this lake's coastline. Usually central basin cores are studied because conditions are more constants. However, Laird & Cumming (2009) proposed that near shore cores are adequate and recommended in reconstructions attempting to infer fluctuations in lake level since shores are mainly concerned in fluctuations of water level.

The vulnerability of the lakeshore to erosion is varied and would depend on slope profile, soil composition, sediment types and compactness (Dearing, 1997). One difficulty of using near-shore cores is that it is possible that part of the sediment archive may be lacking as a result of reworking of previously deposited sediment or wave action (Laird & Cumming, 2009).

On the whole, the present study might contribute to enlarge the background knowledge of paleoclimatic conditions of central Patagonia during the late Holocene.

Understanding changes in ecological systems over long periods of time is essential for placing modern communities in proper context (Delcourt & Delcourt, 1991). When put in a longer context the repeated fluctuations of lake level observed in Colhue Huapi over the last years are part of a recurrent dynamics of the system and should be taken into account in the future management of the water resource and the lake ecosystem sustainability.

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