Biogeochemical processes and the diversity of Nhecolândia lakes, Brazil

TEODORO I.R. ALMEIDA[1], MARIA DO CARMO CALIJURI[2], PATRÍCIA B. FALCO[2],
SIMONE P. CASALI[2], ELENA KUPRIYANOVA[3], ANTONIO C. PARANHOS FILHO[4],
JOEL B. SIGOLO[1] and REGINALDO A. BERTOLO[1]

[1]Instituto de Geociências, Universidade de São Paulo, Rua do Lago, 562, 05508-080 São Paulo, SP, Brasil
[2]Escola de Engenharia de São Carlos, Universidade de São Paulo,
Avenida Trabalhador Sãocarlense, 400, 13566-590 São Carlos, SP, Brasil
[3]Institute of Plant Physiology, Russian Academy of Sciences, Botanicheskaya Street 35, Moscow, 127276, Russia
[4]Centro de Ciências Exatas e Tecnologia, Universidade Federal do Mato Grosso do Sul, Cidade Universitária,
Avenida Costa e Silva, 1524, 79000-060 Campo Grande, MS, Brasil

ABSTRACT

The Pantanal of Nhecolândia, the world's largest and most diversified field of tropical lakes, comprises approximately 10,000 lakes, which cover an area of 24,000 km^2 and vary greatly in salinity, pH, alkalinity, colour, physiography and biological activity. The hyposaline lakes have variable pHs, low alkalinity, macrophytes and low phytoplankton densities. The saline lakes have pHs above 9 or 10, high alkalinity, a high density of phytoplankton and sand beaches. The cause of the diversity of these lakes has been an open question, which we have addressed in our research. Here we propose a hybrid process, both geochemical and biological, as the main cause, including (1) a climate with an important water deficit and poverty in Ca^{2+} in both superficial and phreatic waters; and (2) an elevation of pH during cyanobacteria blooms. These two aspects destabilise the general tendency of Earth's surface waters towards a neutral pH. This imbalance results in an increase in the pH and dissolution of previously precipitated amorphous silica and quartzose sand. During extreme droughts, amorphous silica precipitates in the inter-granular spaces of the lake bottom sediment, increasing the isolation of the lake from the phreatic level. This paper discusses this biogeochemical problem in the light of physicochemical, chemical, altimetric and phytoplankton data.

Key words: Pantanal, alkaline lakes, saline lakes, cyanobacteria, alkalinization processes.

INTRODUCTION

The Pantanal is the largest floodable surface on Earth, covering approximately 200,000 km^2 (Fig. 1). It is located in the Pantanal Basin (Almeida 1945), an inland tectonic depression that originated from tectonic interactions between the South American and Nazca Plates during the Late Tertiary (Assumpção 1998, Ussami et al. 1999). This basin has been filled by several alluvial fans, generating quaternary sediments dominated by quartzose sands, with maximum thickness of approximately 550 m (Assine 2004). The Pantanal is divided

into 11 sub-areas based on characteristics of seasonal floods, physiography and ecology (Silva et al. 1998). Two of these areas, Paiaguás and Nhecolândia, occupy almost the entire alluvial fan of the Taquari River, with an area of 54,125 km^2. This fan is a complex depositional system with an almost circular form approximately 250 km in diameter, the largest on the planet (Assine 2004).

Nhecolândia, whose 24,000 km^2 area occupies the southern half of the Taquari alluvial fan (Fig. 1), has 200 m of altitude in the eastern most part and 80 m near the Paraguay River. This alluvial fan is still active with summer floods. The local annual rainfall is around

Correspondence to: Teodoro Isnard Ribeiro de Almeida
E-mail: talmeida@usp.br

Fig. 1 – Localisation of Pantanal and the studied area (modified from Galvão et al. 2003).

1100 mm, lower than the annual evapo-transpiration rate of 1400 mm (Por 1995). Lower Nhecolândia, which is the study area, corresponds to the oldest depositional lobe of the Taquari alluvial fan (Assine 2004). It is distinguished from other sub-areas of the Pantanal by its uncommon physiography. This is characterised by the presence of seasonally flooded savannas limited by forest fragments growing over elevations 1-3 m in height (known locally as *cordilheiras*) and thousands of lakes with high spatial, physical, chemical and biological variability. These lakes are shallow, and are usually classified according to their pH and electric conductivity (EC; Almeida et al. 2003), pH and salinity (Costa and Telmer 2007), size, degree of roundedness and orientation (E. Fernandes, unpublished data).

The saline lakes, locally named *salinas*, have brackish-to-saline waters and basic pH (often above 10), are rarely deeper than 1 m, with an average depth of approximately 50 cm in the rainy season (Galvão et al. 2003), and rarely become dry. They are distinguished by beaches devoid of vegetation ringed by a fringe of carandas palm trees (*Copernicia alba* Mo-

rang) and Gramineae, which in turn is surrounded by carandas and Bromeliaceae popularly known as "cara-guatá" (*Aechmea* spp.) and finally by the forest that covers the *cordilheiras*. These elevations completely surrounding the *salinas* protect them from the inflow of water during the floods.

The hyposaline lakes, locally named *baías*, are always devoid of beaches, have variable pH and low to-very-low salinity and can surpass 2 m in depth (Furquim et al. 2010), although most lakes are around 1 m in depth (Galvão et al. 2003). Aquatic vegetation is common. While surrounded by *cordilheiras*, the protection of the inflow of waters can be only partial. Carandas are absent from these *cordilheiras*, which have another species of palm tree of equal importance, popularly known as *bocaiúva* (*Acrocomia aculeata* Lodd), which are absent from the *cordilheiras* that surround the *salinas* (Almeida et al. 2003). Also notable are the relative altitudes of the saline and hyposaline lakes: Almeida et al. (2009), using precision equipment, measured the altitude of the 55 lakes studied, finding lower altitudes for the saline ones, and interpreted this as an

evidence of geochemical erosion of sediments through quartz dissolution and reprecipitation of SiO_2 as amorphous silica in the inter-granular spaces. This process occurs only in saline lakes, resulting in their location consistently below their hyposaline neighbours. The depth of the *baías* increases from the margins to the centre, unlike the *salinas*, which have flat sub-horizontal bottoms. This was interpreted by Almeida et al. (2009) as related to the interaction between the alkaline, silica-rich solutions and the weakly acidic water table.

The pH variation is very important, ranging from slightly acid to very basic (Almeida et al. 2003, Costa and Telmer 2007). The salinity also varies strongly, with values of up to 286 times in lakes in relatively restricted geographical areas, according to Costa and Telmer (2007). Considering the sodium content as an indicator of salinity, the maximum difference was 27,145-fold (Barbiero et al. 2008). Such differences are essentially due to the greater isolation of the *salinas* from phreatic recharge by continuous horizons of greenish and grizzly soil of low porosity (Barbiero et al. 2008). Despite these different salinities, Barbiero et al. (2002) and Furquim et al. (2010) concluded that the *salinas* and *baías* waters belong to the same chemical family, excluding the possibility that the salinity is a legacy of past climatic periods. The isolation of the saline lakes is associated with high alkalinity, which helps to attack the quartzose sand and silt, supplying silica (in solution probably as $H_3SiO_4^-$ or $H_2SiO_4^{2-}$) to precipitate Mg silicates (saponite and stevensite), illite and the amorphous silica cementing the grains of quartzose sand. This has been well described by Barbiero et al. (2008) and Furquim et al. (2008).

The lakes of Nhecolândia have some similarity to the soda lakes of the East African Rift Valley, considering the descriptions of Melack and Kilham (1974), Duckworth et al. (1996) and Jones et al. (1998). Like the Rift Valley lakes, the lakes of Nhecolândia have a water deficit (Por 1995, Barbiero et al. 2008). The waters are poor in Ca^{2+} and Mg^{2+} (Barbiero et al. 2002, Furquim et al. 2010), and there are frequent cyanobacteria blooms and an increase in salinity during the dry season (De-Lamonica-Freire and Heckman, 1996, Oliveira and Calheiros, 2000, Medina-Júnior and Rietzeler 2005). It is important to note that the hypothesis that

alkalinisation in the lakes of Nhecolândia originates from carbonate massifs has been completely discarded. A biogeochemical origin, as in the Rift Valley lakes, is the only remaining possible explanation.

De-Lamonica-Freire and Heckman (1996) described 337 planktonic species in the northern part of the Pantanal, verifying a dominance of cyanobacterial species in the dry season and their absence during floods. Because the region is subjected to an intensely dry period between May and October, these authors suggested that the high proliferation of cyanobacteria is associated with increases in salinity, but did not show a relation between the bloom of these organisms and pH, although there was a positive correlation with salinity, as is normal in alkaline lakes. In their quantitative study of the plankton species of the Paraguay River and its flood plains, Oliveira and Calheiros (2000) identified 82 species. Similar to De-Lamonica-Freire and Heckman (1996), these authors found that Chlorophyceae were prevalent and Cyanobacteriae were present only in the dry season. These studies confirm the general rule of nature, that the more severe the environmental conditions, the lower the biodiversity and the denser the population of surviving organisms (Sergeev et al. 2002) This explains the prevalence of cyanobacterial extremophiles in the saline waters of Nhecolândia, as observed in all prior studies (Oliveira and Calheiros 2000, Santos et al. 2004, Medina-Júnior and Rietzeler 2005, G. Mourão, unpublished data). The high evaporation rate during the dry season and the simultaneous biochemical processes (mainly the absorption of CO_2 by phytoplanktonic productivity) increase the salinity and alkalinity to adverse levels for most phytoplanktonic species. Since the prevalence of any species in an environment depends on its superior survival ability (Tilman 1977), only the more resistant species will survive in high salinities and pHs. Cyanobacteria tend to occupy more ecologically adverse niches (Esteves 1998), and thereby have a higher survival ability. This explains why they were probably the first organisms to appear on Earth, as evidenced by fossils in rocks of 3.5 to 3.8 Ga (Westall 2005). The high proliferation level of cyanobacteria is explained by the absence of competitors; their resistance to high salinity, high temperatures and low oxygen levels (Silva et al. 2008); their freedom

from zooplankton predation; their accessory pigments such as phycobilins, which increase their capacity to absorb solar electromagnetic radiation in the green wavelength; and their ability to control their buoyancy and thereby migrate through the water column to enhance their photosynthetic activity (Shapiro 1990). It has been observed that shallow lakes favour the development of dense phytoplanktonic populations and that the *salinas* are shallower than the *baías* (Galvão et al. 2003). It is evident that in Nhecolândia there is a correlation between pH and salinity (Almeida et al. 2003, Galvão et al. 2003, Costa and Telmer 2007). This indicates that the alkalinisation and salinisation processes are interdependent. A correlation between salinity and phytoplanktonic activity has been described, but the possibility of cause and effect relationships among the alkalinity, salinity and phytoplanktonic activities has not been discussed in the literature.

The available data indicate that the Nhecolândia physiography arises from the complex and only partially understood combination of biological, hydrological, climatic, sedimentary, geochemical and neotectonic processes. To explain the diversity of lakes, however, we propose a hybrid process based on the phytoplankton activity and hydrogeochemistry of the saline and hyposaline lakes.

ALKALINE LAKES AND THE BIOGEOCHEMICAL PROCESSES INVOLVED

The geochemistry of calcium and its carbonates has a fundamental role in the preservation of the pH balance in waters: pH is increased through the dissolution of carbonates (releasing HCO_3^{2-} and CO_3^{2-} species into the water) and reduced through the precipitation of $CaCO_3$ (removing CO_3^{2-} from water). Hence, the condition of neutral pH, that is conducive for most terrestrial organisms, is attained in the presence of calcium, which stabilises the pH between 5.5 and 8.5 (Zavarzin 2002). According to this author, three routes of calcium capture can be considered: (1) abiotic chemical precipitation of carbonates of calcium, caused by physical and chemical imbalance in the water, such as the saturation of the solution because of evaporation; (2) a biological route where the carbonate precipitation is caused by the alkaline barrier created by the activity of microorganisms; and (3) direct precipitation in the construction of skeletons by intracellular mineralisation. The dissolution of the carbonates is caused by reverse processes: an increase in CO_2 concentration by respiration in the oxygenated zone, or by the anaerobic generation of organic acids.

Soda lakes constitute the most natural alkaline environment on the planet, with pHs as high as 12. The formation of such lakes requires low Ca^{2+} and high Na^{2+} contents, tropical arid or semi-arid zones with a water deficit, and salinisation through evaporation. The increase in the alkalinity is due to the disequilibrium in the $CO_2/ HCO_3^-/ CO_3^{2-}$ system to CO_3^{2-} arising from the impossibility of precipitating $CaCO_3$ (Duckworth et al. 1996). The persistence of alkaline lakes, however, requires a continuous process of alkalinisation to annul the buffering effect of CO_2 (Jones et al. 1998). In agreement with McConnaughey and Whelan (1997), the most elementary mechanism of photosynthetic alkalinisation of water results from the liquid capture of CO_2, leading to the concentration of CO_3^{2-} and OH^-. If the water is oversaturated with $CaCO_3$, precipitation is induced biogeochemically, with a resulting drop in pH to near neutrality and an enrichment of Na^+ and Cl^- in the solution. By contrast, high primary photosynthetic productivity, mainly due to a dense cyanobacterial population during blooms, will bring a decrease in the dissolved HCO_3^- and thereby a biogenic enrichment in CO_3^{2-}. With a deficiency in Ca^{2+} to precipitate $CaCO_3$, the pH necessarily rises (Visscher et al. 1998). Thompson and Ferris (1990), using cultures of *Synechococcus*, a cyanobacterium, demonstrated the pericellular precipitation of gypsum, calcite and magnesite parallel to an increase of the pH from 7.97 to 8.57 in 72 hours. This is a fast rate of alkalinisation, although in the experiment there were Ca^{2+} and Mg^{2+} present to minimise the pH increase.

Until recently, the enzyme carbonic anhydrase (CA) was known as an enzyme that catalyses the reversible hydration of CO_2 ($CO_2 + H_2O \leftrightarrows HCO_3^- + H^+$) in many eukaryotes. Close to the end of the 1990s it was discovered to be much more common and omnipresent in the domains of Archaea and Bacteria (Smith et al. 1999). Some eukaryotic algae can precipitate intracellular $CaCO_3$ through the activity of CA. However, the

cyanobacteria promote this activity only pericellularly. The internal pH of these organisms is neutral – their CA promotes external alkalinisation by OH^- excretion, whereas fixing CO_2 from HCO_3^- generates pericellular $CaCO_3$ precipitation (Kupriyanova et al. 2007). In other words, cyanobacteria promote the intense capture of inorganic carbon in the form of CO_2 or HCO_3^- not only by photosynthetic activity during blooms (similar to other microorganisms), but also by the extra cellular activity of CA, which alkalinises their environment. For this reason, these organisms are particularly efficient in raising the pH of the water. According to Kupriyanova et al. (2007), the intensity of cyanobacterial CA activity is strictly controlled by pH, with a maximum at pH 9.8, which is the ideal pH for these organisms. Thus, at pH > 9.8 the CA probably becomes increasingly less effective at raising alkalinity.

MATERIALS AND METHODS

Lakes were chosen for sampling using remote sensing images whose spectra were influenced by the phytoplankton content (Galvão et al. 2003). Real-colour TM-Landsat 5 and AVNIR2-ALOS images were employed.

Three field campaigns were conducted to collect water samples in different seasons. Initially, these studies were planned for the same group of lakes at the Rio Negro farm, but only one set of water samples could be collected there, so the other two sets were acquired from the neighbouring Barranco Alto farm. The first set of samples was collected from 18 to 25 August 2007, in the middle of a rigorous drought. The second collection period was from 10 to 19 July 2008, at the beginning of drought, as the rainy season had extended into June. The third was from 6 to 10 October 2008, at the end of the normal dry season, but in a less intense drought than that of August 2007.

The three different groups of data are independent, considering the dynamics of the environment. At the same time, it was possible to compare a sub-set of samples, collected at two different climatic situations, from the same group of lakes. Finally, although the ensemble had problems (being sampled over two years), it is possible to consider three sets of samples: those taken at the beginning (July 2008), the middle (October 2008) and the end of the dry season (August 2007).

The temperature of the water (°C), the EC ($\mu S.cm^{-1}$), the dissolved oxygen (% and $mg.L^{-1}$) and the pH were measured *in situ* with a multi-probe instrument (Yellow Springer, 556 MPS). Samples of water were collected close to the centre of the lakes in polyethylene flasks, filtered with Millex filters with a 0.45 membrane and then frozen. The samples of the first campaign were taken to the Laboratory of Groundwater Research Centre at the Institute of Geosciences of São Paulo University (USP) for cations analysis. Na^+ and K^+ were analysed by flame photometry, and the other cations by atomic absorption spectrophotometry. The samples from the two other collection sets were sent to Activation Laboratories (Toronto, Canada) for similar cation analysis by ICP-OES or ICP-MS, according to the salinity identified in the field by EC. The anions were analysed by ion chromatography in the laboratories of the Engineering School of São Carlos (USP).

For the determination of phytoplankton, the water samples were collected and fixed with an acetic Lugol solution. The phytoplankton was counted using the sedimentation method (Uthermohl 1958). From the quantitative analysis, the total density (organisms.mL^{-1}) was calculated according to the equation below (APHA 1995):

$$D_{(\text{org/mL})} = \frac{C \times At}{Af \times F \times V}$$

where

D = total density (organisms.mL^{-1});
C = number of organisms counted;
At = total surface area of the sedimentary bed (mm^2);
Af = surface area of the field of counting (mm^2);
F = number of counted fields;
V = volume of the sediment (mL).

The relative abundance was estimated considering the number of individuals of each species and the total number of individuals, according to the classification of McCullough and Jackson (1985): 50 to 100%, dominant organisms; 30 to 49%, abundant organisms; 10 to 29%, common organisms; 1 to 9%, occasional organisms; <1%, rare organisms.

To determine the concentrations of chlorophyll *a* and pheophytin, the samples were filtered through glass microfibre membranes (Millipore AP 20; 47 mm diameter and 8.0 μm porosity), and stored frozen until the

TABLE I
Classification by EC (μS.cm^{-1}) adopted for the lake waters studied and the approximate content of total dissolved solids (TDS) calculated by the mean value reported in APHA (1995).

Classes of waters	EC (μS.cm^{-1})	Approximated TDS (g.L^{-1})
Freshwater	< 100	< 0.06
Water with low or average salinity	100 to 750	0.06 to 0.5
Water with high salinity	750 to 2250	0.5 to 1.4
Water with very high salinity	2250 to 5000	1.4 to 3.1
Hypersaline water	> 5000	> 3.1

moment of extraction. Ethanol at 80% was used for the extraction. The spectrophotometric analysis of the extracts was performed according to APHA (1995), and the reading was done between wavelengths of 665 and 750 nm. For the determination of chlorophyll a (μgL^{-1}) and pheophytin (μg.L^{-1}), the following formulas were used as in Nush (1980):

$$\text{Chlorophyll } a = 29.6$$
$$\times \{(Eu_{665} - Eu_{750}) - (Ea_{665} - Ea_{750})\} \quad (1)$$
$$\times v/V \times s$$

$$\text{Pheophytin} = 29.6$$
$$\times \{[1.7 \times (Ea_{665} - Ea_{750})] - (Eu_{665} - Eu_{750})\} \quad (2)$$
$$\times v/V \times s$$

where:
Eu = absorbance of the unacidified sample;
Ea = absorbance of the acidified sample;
v = volume of the bed (mL);
V = volume of the filtered sample (L);
s = thickness of the cuvette (cm);
29.6 = specific absorption coefficient of chlorophyll a;
1.7 = ratio of the yield of unacidified to acidified chlorophyll a.

The quantitative and qualitative analyses of the phytoplankton and chlorophyll concentrations were done in the Laboratory of Biotoxicology of Continental Waters, of the USP School of Engineering, São Carlos campus.

The Rio Negro farm samples were given the general acronym RN, added to the lake code according to the sampling order, and the letter "s" for *salinas* or "b" for *baías*. Samples from the Barranco Alto farm have only the BA acronym followed by the lake number. All water samples were classified by their EC proportional to the salinity according to Table I, modified from the classification by USSL (1954).

RESULTS AND DISCUSSION

In August 2007 at the Rio Negro farm, water from 15 lakes was sampled for limnological and hydrogeochemical analyses. Eight of these lakes were *salinas* (EC > 750 μS.cm^{-1}). In July 2008, 28 lakes were sampled, of which 14 were *salinas*. In October 2008, 19 lakes were sampled for hydrogeochemistry and 14 for limnological analyses, of which seven were EC < 750 μS.cm^{-1} and 12 EC > 2,000 μS.cm^{-1}. The results of the chemical analyses showed that all the waters were extremely poor in Ca^{2+} and Mg^{2+} but, in the *salinas,* rich in Na$^+$ and K$^+$, as stated in the general literature (Zavarzin 2002) and that on Nhecolândia (Barbiero et al. 2002, Furquim et al. 2008). Table II presents the results of the August 2007 sampling, where the poverty in Ca^{2+} and Mg^{2+}ions is clear. The independence of these cations with regard to EC and pH is evident. The Na and K cations have a high correlation with EC, as expected, it being almost perfect in the case of Na$^+$ if we ignore sample RN7S (R^2 = 0.9997).

The fieldwork at the Barranco Alto estate, in July and October 2008 yielded similar results (Table III). For most of the water samples with a high pH, the content of dissolved calcium was below the detection limit, as expected, because, in these conditions, Ca^{2+} precipitates as CaCO$_3$. It is important to observe that the high Na$^+$ and K$^+$ content occurred only in the saline lakes because of evaporation from the lakes, which are isolated from phreatic recharge. As regards the phytoplanktonic

TABLE II
EC, pH and content in mg.L^{-1} of Ca^{2+}, Mg^{2+}, Na$^+$ and K$^+$
of samples from the Rio Negro farm lakes (August 2007).

Lake	EC μS.cm^{-1}	pH	Ca	Mg	Na	K
			mg.L^{-1}			
RN1B	30	8.11	2.8	2.0	8.3	6.7
RN1S	2858	9.41	3.7	0.14	906	340
RN2B	74	8.52	5.1	4.5	12.3	9.5
RN2S	3467	9.06	6.6	4.1	1060	245
RN3B	110	7.13	4.6	4.8	23.1	17.2
RN3S	2429	9.7	4.7	0.15	762	293
RN4S	2798	9.37	4.1	3.1	813	155
RN5B	591	7.32	4.2	8.1	152	36.1
RN5S	7156	9.4	2.9	0.26	2222	478
RN6B	42	8.28	1.8	2.0	4.7	9.4
RN6S	11500	9.41	11.0	0.91	3600	805
RN7B	27	7.33	0.98	1.1	7.5	4.9
RN7S	8572	9.51	4.5	1.0	1353	280

material, 28 lakes (*salinas* and *baías*) were sampled in the first round and 19 in the second.

Table IV shows the percentages of lakes in relation to the classes of the prevalent phytoplanktonic organisms in each of the five classes of water as described in Table I. The 61 samples, as well as each contemporaneous set, confirm the conclusion of Oliveira and Calheiros (2000), Santos et al. (2004), Oduor and Schagerl (2007) and Santos and Sant'Anna (2010) that cyanobacteria are more prevalent in more saline waters. When the results from the same groups of lakes sampled in July and October 2008 are compared, the seasonal variations replicate the findings of other authors. The sampling of August 2007 does not represent a climatically intermediate situation, as indicated by the salinity and stable isotope data, possibly reflecting climatic differences between 2007 and 2008. Two readings could be made from Table IV: the seasonal evolution and, for each sample collection, the distribution of classes of organisms as a function of salinity. For the July 2008 collection, a continuous increase in the proportion of cyanobacteria was observed in relation to the salinity. For the August 2007 sample collection, the distribution was irregular, though with a clear tendency towards the growing dominance of cyanobacteria in the high-salinity lakes. However, this does not give an intermediary

view between the sample collections of July and October 2008. These data show the difficulty in comparing, for detailed observations, different lakes and sample collections from different years. We were surprised to find, among the high salinity lakes, with EC$>$5000μS.cm^{-1}, a lake with a predominance of Bacillariophyceae rather than Cyanobacteriae. Finally, for the October 2008 collection, normally the most adverse situation because it would be at the end of the dry season, cyanobacteria were prevalent even in lakes with low-to-medium salinity. However, Chlorophyceae were dominant in a lake of high salinity. The seasonal tendency is clear for the sample collections taken from the same lakes; namely, there is an increase of cyanobacterial dominance during the dry season. In relation to the salinity, the water classes have the same tendency, with the prevalence of cyanobacteria in the most saline waters. Considering the number of genera and species (Table V), the tendency for the increase of cyanobacteria is continuous from the freshwater to very saline waters. However, there is an unexpectedly reduced presence of cyanobacteria in the hypersaline water class.

The diversity of phytoplankton and the proportion of cyanobacteria in relation to all phytoplankton organisms are, in general, highly correlated to water classes from Table I (Tables VI and VII). The low number of

TABLE III
EC, pH and content in mg/L of Ca^{2+}, Mg^{2+}, Na^+ and K^+ of samples from the Barranco Alto farm lakes in July and October 2008.

Lake	First sampling (July 2008)						Second sampling (October 2008)					
	EC uS/cm	pH	Ca mg/L	Mg mg/L	Na mg/L	K mg/L	EC uS/cm	pH	Ca mg/L	Mg mg/L	Na mg/L	K mg/L
BA01	25	6.02	1.4	0.8	2.1	3.6	36	7.89	1.7	0.848	1.53	4.27
BA02	113	7.09	4.3	2.3	12.4	13.6	161	8.35	4.6	1.62	22	17.5
BA03	172	7.77	4.6	2.6	22.3	17.9	229	8.77	6.3	1.95	40.1	19.8
BA04	77	4.88	2.5	0.6	22.8	5.4	–	–	–	–	–	–
BA05	3185	9.3	< 0.6	0.29	744	128	4567	9.21	< 0.6	0.57	871	148
BA07	2932	9.31	< 0.6	0.99	803	178	5641	9.6	< 0.6	1.21	1130	250
BA08	27	5.89	0.7	0.4	5.2	3	–	–	–	–	–	–
BA09	4140	9.44	< 0.6	5.56	837	148	6607	9.67	< 0.6	3.19	1330	198
BA12A	1045	8.71	< 0.6	0.74	14.6	3.9	–	–	–	–	–	–
BA12B	1160	8.98	7.4	2.15	0.448	98.2	–	–	–	–	–	–
BA14	2517	9.49	< 0.6	0.45	542	166	–	–	–	–	–	–
BA16	3618	9.46	12	1.16	1320	359	8410	9.77	13	2.87	1680	430
BA21	7188	9.33	15	1.97	2730	324	16360	9.78	22	4.05	3340	799
BA22	5357	9.25	< 0.6	1.69	1770	207	12870	9.67	< 0.6	1.57	2410	597
BA23	40	6.74	2.8	0.8	9.6	5	79	5.69	3.4	0.956	13.7	6.63
BA24	1590.5	9.38	13	1.75	527	139	3976	10.06	11	2.8	843	159
BA25	710	9.28	< 0.6	0.41	260	103	2317	9.68	< 0.6	0.71	332	141
BA26	2671	9.5	12	1.41	980	227	6857	9.85	25	3.85	1540	342
BA27	10	6.5	0.6	0.4	2.8	2.8	67	6.9	2.5	0.98	5.72	5.37
BA30	81	7.69	5.9	2.3	16.2	19	225	6.35	2.2	0.867	15.8	37.7
BA31	95	6.5	2.1	1.08	18.2	34	170	8.69	6.8	2.73	14.5	20.2
BA32	154	7.74	5.5	3.2	35.9	29.5	–	–	–	–	–	–
BA33	438	9.52	1.9	0.2	356	110	–	–	–	–	–	–
BA34	1001	9	2.9	0.26	0.321	158	–	–	–	–	–	–
BA35	780	9.09	< 0.6	1.23	229	196	2032	9.45	< 0.6	1	199	191
BA36	940	8.89	3.7	1.42	0.316	111	2116	9.19	< 0.6	0.84	320	128
BA37	1750	9.28	< 0.6	0.28	600	127	3940	7.98	< 0.6	0.47	791	173
BA40	36	7.89	1.8	0.911	2.5	6.26	–	–	–	–	–	–

genera and species in the freshwater lakes could be because more complete limnological data were taken from only one freshwater lake, thereby artificially reducing the diversity. For the other classes, the pattern of diversity reduction with salinity increase is clear, above all when all data are considered. It is clear that this cyanobacteria association is more prevalent in more saline waters, except for the hypersaline class (Table VI and VII). In the latter, only cyanobacteria were expected, because they are extremophiles organisms, thus more adaptable at a hypersaline environ-

ment. However, they have a lesser presence than in the highly saline class lakes, yielding more space for Chlorophyceae and Cryptophyceae (Table V). If this situation was observed in only one field campaign, it might be considered an exception. Because it was seen in all three field campaigns, it suggests an unexpected and unexplained trend. Table VII shows that, for the other salinity groups, there is a distinct increase in cyanobacterial dominance from the beginning to the end of the dry season except in the hypersaline waters, where their dominance remained the same.

TABLE IV

Distribution of the percentage of classes of prevalent phytoplankton organisms in relation to the total number of phytoplanktonic classes described for the groups of lakes classified according to Table I. Cyanobacteria = Cyano; Chlorophyceae = Chloro; Bacillariophyceae = Bacill; Cryptophyceae = Crypto; Dinophyceae = Dinophy.

Class of water	Class of prevalent organisms (% of lakes)				
	Cyano	Chloro	Bacill	Crypto	Dinophy
Freshwater (July 2008) n = 7	25	25	0	50	0
Freshwater (August 2007) n = 4	50	25	0	0	25
Freshwater (October 2008) n = 1	25	75	0	0	0
Average for freshwater	**33.3**	**41.7**	**0.0**	**16.7**	**8.3**
Low to average salinity (July 2008) n = 5	66	33	0	0	0
Low to average salinity (August 2007) n = 3	0	33	0	66	0
Low to average salinity (October 2008) n = 4	100	0	0	0	0
Average of low to average salinity	**55.3**	**22.0**	**0.0**	**22.0**	**0.0**
High salinity (July 2008) n = 8	75	25	0	0	0
High salinity (August 2007) n = 0	*	*	*	*	*
High salinity (October 2008) n = 4	87.5	12.5	0	0	0
Average of high salinity	**79.2**	**18.8**	**0.0**	**0.0**	**0.0**
Very high salinity (July 2008) n = 6	80	20	0	0	0
Very high salinity (August 2007) n = 4	50	25	25		0
Very high salinity (October 2008) n = 4	100	0	0	0	0
Average of very high salinity	**76.7**	**15.0**	**8.3**	**0.0**	**0.0**
Hypersaline (July 2008) n = 2	100	0	0	0	0
Hypersaline (August 2007) n = 4	75	0	25	0	0
Hypersaline (October 2008) n = 1	100	0	0	0	0
Average of hypersaline	**91.7**	**0.0**	**8.3**	**0.0**	**0.0**

Analysis of the density of organisms in the two sample collections from the Barranco Alto farm with the EC and pH data (Table VIII) demonstrated two different behaviours. The freshwater lakes with the phreatic recharge had a small increase in salinity with increased pH, essentially because of the activity of microorganisms. The lakes with saline water had a pH increase related to more intense activity of microorganisms, including blooms, but with a large increase in salinity because of evaporation. The greatest geochemical imbalance was caused by intense evaporation over lakes that are necessarily isolated from the water table. It was observed that:

(1) in the sample collections at the end of the dry season, three lakes showed cell densities > 10^6;

(2) these lakes have higher pHs;

(3) the lakes with higher EC had a low density of organisms at the beginning of the dry season and the greatest density at the end of dry season;

(4) the highest pH in the samples collected at the end of the dry season was related to an EC far lower than that of the lakes with pH > 9.

These data enable us to visualise the existence of two independent processes that increase the lakes' pH, as proposed by Zavarzin (2002): (1) increasing salinity through evaporation (directly associated to the degree of isolation of the lake from the phreatic recharge); and (2) the increasing density of organisms (directly associated to the high proliferation rate of phytoplankton). The BA21 lake at the beginning of the dry season had a high pH and the highest EC of the sampled group. With the EC increasing towards the highest value found in all the campaigns (and therefore the highest salinity), the isolation of this lake and the favourable conditions for an intense phytoplankton bloom are clearly evident. This bloom was probably partly responsible for the increase in pH, because the EC increased 2.3 fold (a sim-

TABLE V
Number of genera and species described by salinity of water classes adopted (G = Genus; sp = species).

Class of organisms		Class of water (all the lakes)				
		Freshwater	Low to average salinity	High salinity	Very high salinity	Hypersaline
Cyanobacteria	G	8	9	15	23	6
	sp	8	13	20	27	7
Chlorophyceae	G	25	27	16	0	6
	sp	33	44	17	0	6
Bacillariophyceae	G	5	4	–	6	0
	sp	5	4	0	6	0
Cryptophyceae	G	2	3	9	0	3
	sp	2	3	9	0	3
Dinophyceae	G	1	2	0	1	0
	sp	1	2	0	1	0
Chrysophyceae	G	1	1	0	0	0
	sp	1	1	0	0	0
Euglenophyceae	G	3	3	0	3	0
	sp	3	3	0	3	0
All the organisms	G	45	49	40	33	15
	sp	53	70	46	37	16

TABLE VI
Number of species of phytoplanktonic organisms observed in the lake samples from the Rio Negro farm and the relative percentage of cyanobacteria. Sampling was done in August 2007.

Class of water	All species	% Species of cyanobacteria
Freshwater (four lakes)	52	15
Low to average salinity (three lakes)	69	19
High salinity (five lakes)	46	43
Very high salinity (four lakes)	37	73
Hypersaline (two lakes)	16	44

TABLE VII
Species of phytoplankton observed in the lake samples from the Barranco Alto farm and the relative percentage of cyanobacteria. The first sample collection was done in July 2008 and the second in October 2008.

Class of water	All species		% Species of cyanobacteria	
	1st sampling	2nd sampling	1st sampling	2nd sampling
Freshwater	11	9	9	44
Low to average salinity	28	31	25	29
High salinity	18	24	22	58
Very high salinity	15	17	87	100
Hypersaline	9	12	44	44

TABLE VIII
Density of organisms, EC and pH of the samples of October 2008.
The highest pHs are related to the highest density of organisms in extreme dryness
(bold characters and grey lines). Data ordered by pH of the second sampling.

	Density of organisms (org.mL^{-1})		First sampling		Second sampling	
			EC	pH	EC	pH
Lakes	First sampling	Second sampling	μS.cm^{-1}		μS.cm^{-1}	
BA37	61,726	119,019	1750	9.28	3940	7.98
BA2	23,493	13,727	113	7.09	161	8.35
BA31	630	35,141	95	6.5	170	8.69
BA3	27,178	144,697	172	7.77	229	8.77
BA36	148	284	940	8.89	2116	9.19
BA5	354,695	12,319	3185	9.3	4567	9.21
BA35	51,795	212,641	780	9.09	2032	9.45
BA7	204,986	257,568	2932	9.31	5641	9.6
BA9	23,402	95,077	4140	9.44	6607	9.67
BA25	18,759	6,909	710	9.28	2317	9.68
BA16	**1,032,990**	**2,763,854**	**3618**	**9.46**	**8410**	**9.77**
BA21	**123,256**	**10,443,842**	**7188**	**9.33**	**16360**	**9.78**
BA24	**401,862**	**1,020,323**	**1591**	**9.38**	**3976**	**10.06**

ilar pattern to the average of all the lakes – 2.1 times), whereas the density of organisms increased 85 fold. This suggests that two processes act to increase the pH and alkalinity: one geochemical and other biogenic. Analysis of the densities of organisms in lakes BA16, BA21 and BA24 show that the latter had the highest pH of the group and the lowest density of organisms. The data could indicate that, in this case, the alkalinisation was simply dominated by physicochemical processes, such as evidenced by the geochemical imbalance in evaporation. Another possibility is that when the pH attain the peak of 9.8, there are a fall in CA activity, reducing the productivity of these organisms. Both hypotheses could explain a small increase in the cyanobacterial population in the most alkaline lake, with a pH > 10, but the latter seems more convincing because the EC of lake BA24 was not particularly high.

Arranging the data according to the population density of the organisms, the six lakes with density $> 150,000$ org.mL^{-1} coincided with the five lakes with the highest pHs and with five of the eight lakes with a EC > 750 gS.cm^{-1}, indicating a significant correlation (Table IX). By contrast, the lake with the highest EC had one of the lowest densities of organisms, and one of the lakes with the highest density of organisms had one of the lowest ECs, an evidence that phytoplankton blooms are not strictly dependent on EC (or salinity). However, ordering the data by pH, the five highest pHs were associated with five of the six highest microorganism densities. Finally, in these two groups of independent data (the lakes from the Rio Negro and Barranco Alto farms), the highest densities were linked to the highest salinities, suggesting that the most intense blooms occur in those lake waters more isolated from the phreatic zone. The fact that all the studied lakes with pH > 9.0 in October had very high salinity or hypersalinity suggests a causal relationship between the processes of isolation and alkalinisation of these lakes.

In the August 2007 fieldwork data (Table X), there is an evident correlation between the chlorophyll and pheophytin pigments with pH. Considering that only cyanobacteria have pheophytin and that organisms of other classes were described in all the classes of water, the sum of these two pigments was considered more representative of the biogenic contribution to increased pH.

The data concerning pigments in the samples of the fieldworks of 2008 are clear (Table XI). In the two sample collections, there were two contrasting groups of samples: those with low pigment levels and those

TABLE IX

**Density of organisms, EC and pH of the August 2007 sampling. The data are
ordered by pH on the left and by EC on the right. The highest pHs are related to
the highest density of organisms, and there is a greater independence from EC.
The data showing the higher density of organisms, pH and EC are in bold characters.**

Lake	Density of organisms org.mL^{-1}	pH	EC μS.cm^{-1}	Lake	Density of organisms org.mL^{-1}	pH	EC μS.cm^{-1}
RN 3b	300	7.13	110	RN 7b	1100	7.33	27
RN 4b	900	7.17	286	RN 1b	12900	8.11	30
RN 5b	84800	7.32	591	RN 6b	3200	8.28	42
RN 7b	1100	7.33	27	**RN 2b**	**164400**	**8.52**	**74**
RN 1b	12900	8.11	30	RN 3b	300	7.13	110
RN 6b	3200	8.28	42	RN 4b	900	7.17	286
RN 2b	**164400**	**8.2**	**74**	RN 5b	84800	7.32	591
RN 8s	700	9.03	12593	RN 3s	649500	9.7	2429
RN 2s	2900	9.06	3467	RN 4s	1059	9.37	2798
RN 4s	1059	9.37	2798	**RN 1s**	**150200**	**9.41**	**2858**
RN 5s	**423400**	**9.4**	**7156**	RN 2s	2900	9.06	3467
RN 1s	**15020**	**9.41**	**2858**	**RN 5s**	**423400**	**9.4**	**7156**
RN 6s	**5914600**	**9.41**	**11500**	**RN 7s**	**159400**	**9.51**	**8572**
RN 7s	**159400**	**9.51**	**8572**	**RN 6s**	**5914600**	**9.41**	**11500**
RN 3s	**649500**	**9.7**	**2429**	RN 8s	700	9.03	12593

TABLE X

**Pigments in phytoplankton (chlorophyll *a* and pheophytin),
pH and EC. Bold characters: samples with pH > 9. The data
are ordered by the sum of the chlorophyll *a* + pheophytin values.**

Lake	Chl *a*	Pheo	Chl *a* + pheo	pH	EC μS.cm^{-1}
	μg.L^{-1}				
RN 4b	4.44	4.37	8.81	7.17	286
RN 3b	2.22	6.59	8.81	7.13	110
RN 2b	10.36	2.07	12.43	8.52	74
RN 7b	14.06	7.44	21.50	7.33	27
RN 7s	**21.90**	**4.20**	**26.10**	**9.51**	**8572**
RN 1b	23.68	7.4	31.08	8.11	30
RN 6b	18.94	15.87	34.81	8.28	42
RN 2s	**22.20**	**15.10**	**37.30**	**9.06**	**3467**
RN 5b	22.69	18.06	40.75	7.32	591
RN 4s	**29.60**	**18.75**	**48.35**	**9.37**	**2798**
RN 8s	**29.6**	**28.42**	**58.02**	**9.03**	**12593**
RN 5s	**51.06**	**10.06**	**61.12**	**9.4**	**7156**
RN 3s	**231.9**	**123.8**	**355.7**	**9.7**	**2429**
RN 1s	**237.9**	**120.9**	**358.87**	**9.41**	**2858**
RN 6s	**2836**	**554.1**	**3390**	**9.41**	**11500**

TABLE XI

Contents of chlorophyll *a*, pheophytin, pH and EC of the samples collected in July (first sampling) and October 2008 (second sampling). Both tables are ordered by pH. Bold characters: the samples in which the sum of the pigment values is significant.

	First sampling					Second sampling				
Lakes	Chl	Pheo	Chl + Pheo	pH	EC	Lakes	Chl	Pheo	Chl + Pheo	pH	EC
	μg.L^{-1}				μS.cm^{-1}		μg.L^{-1}				μS.cm^{-1}
BA31	2.1	1.8	3.9	6.5	95	BA37	20.2	12	32.2	7.98	3940
BA2	38.4	18.8	57.2	7.09	113	BA2	33.5	7.5	41	8.35	161
BA32	30.7	6.9	37.6	7.74	154	BA31	14.7	2.4	17.1	8.69	170
BA3	27.9	6.3	34.2	7.77	172	BA3	34.9	7.4	42.3	8.77	229
BA13	3.5	2.1	5.6	8.69	785	BA36	2.8	–		9.19	2116
BA12A	1.4	2	3.4	8.71	1045	BA5	15.4	7.6	23	9.21	4567
BA36	6	5.2	11.2	8.89	940	BA35	82.3	17.8	100.1	9.45	2032
BA12B	120	26.5	146.5	8.98	1160	BA7	51.6	19.2	70.8	9.6	5641
BA34	162.5	34.2	196.7	9	1001	BA9	−1	−1	−2	9.67	6607
BA35	17.1	3.6	20.7	9.09	780	BA22	25.1	8.1	33.2	9.67	12870
BA22	**2594.7**	**530.1**	**3124.8**	**9.25**	**5357**	BA25	18.1	6.8	24.9	9.68	2317
BA25	19.5	4.9	24.4	9.28	710	**BA16**	**2399.4**	**4895.1**	**7294.5**	**9.77**	**8410**
BA37	23.7	3.6	27.3	9.28	1750	**BA21**	**2976**	**956**	**3932**	**9.78**	**16360**
BA5	27.9	8.7	36.6	9.3	3185	**BA26**	**1004.4**	**1812.8**	**2817.2**	**9.85**	**6857**
BA7	25.1	11.5	36.6	9.31	2932	**BA24**	**5003.4**	**2287.8**	**7291.2**	**10.06**	**3976**
BA21	**5761.4**	**1738.2**	**7499.6**	**9.33**	**7188**						
BA24	**3325.7**	**873.3**	**4199**	**9.38**	**1591**						
BA9	23	6.8	29.8	9.44	4140						
BA16	17.4	7	24.4	9.46	3618						
BA14	152.5	28.5	181	9.49	2517						
BA26	**1735.4**	**471.5**	**2206.9**	**9.5**	**2671**						
BA33	4.2	2.2	6.4	9.52	438						

with very high levels. In the July sample collection at the beginning of the dry season, there was no correlation between pigment content and pH, indicating that the action of the microorganisms during this period did not significantly influence the pH. For the samples collected in October 2008 at the end of the dry season, the samples with high pigment content corresponded to the highest pHs. The interpretation seems to be clear: the action of the phytoplanktonic organisms to increase the pH occurs in the dry season, concomitant to the blooms, as observed.

Evaporation, in an environment with a water deficit, will cause intense salinisation in the lakes isolated from phreatic recharge. Most of the lakes (those that remain with fresh water all year round) interact with the phreatic zone and thereby do not suffer an intense salinisation. The diversity of the lakes of Nhecolândia

in colouration (in the function of microorganisms), the presence or absence of sand beaches (the high salinity of the *salinas* hinders the growth of Gramineae), the presence of macrophytes (which do not survive in saline waters) and the lower topographic level of the *salinas* in relation to the neighbouring *baías* could be explained by the biogeochemical process presented here.

Chemical analyses of the water sampled in July and October of 2008 revealed negative values of saturation indexes for amorphous silica in all samples from the *baías* (Fig. 2), which indicates undersaturation of the solutions, and values close to zero for the samples from the *salinas*, indicating a predominant condition of chemical equilibrium between the dissolved and mineral states. Such conditions favour the formation of amorphous silica, especially during the dry season. The *salinas*' basal substrate, composed of a framework of
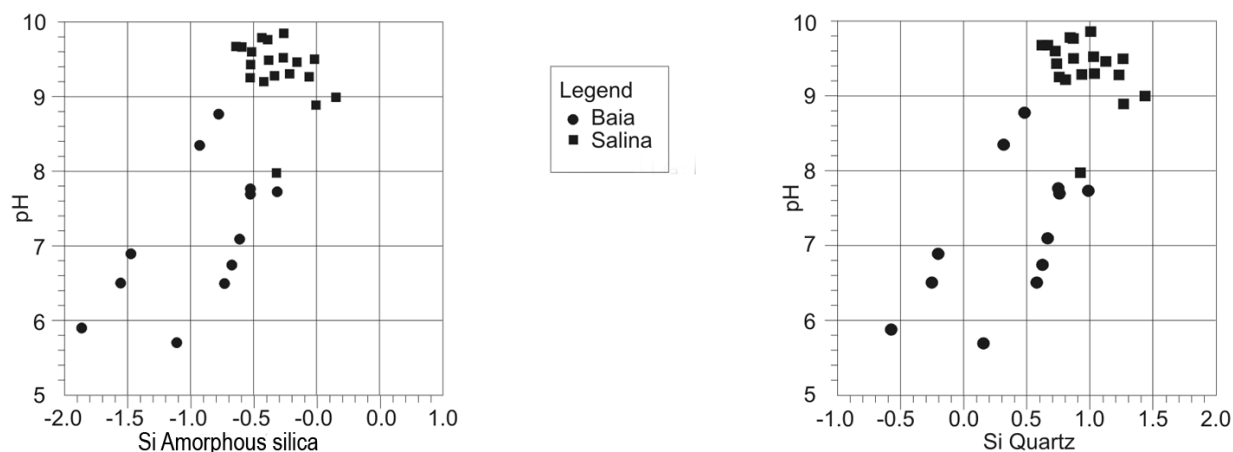
Fig. 2 – Stability of pH × amorphous silica (left) and quartz (right) diagram. Modified from Freeze and Cherry's (1971).

quartz sand and a cement of amorphous silica, is extremely impermeable. This promotes hydraulic isolation of the lake from the shallow and locally confined aquifer waters. Figure 2 also indicates that the amorphous silica was in chemical equilibrium with the water samples collected from *salinas* in July 2008, at the beginning of the dry season. Samples taken in October 2008 (at the end of the dry season) had a higher content of total dissolved solids, but lower concentrations of dissolved silica, as well as relatively lower saturation of amorphous silica, indicating that an removal of silica from the solution to the solid phase, during the monitoring period, probably occurred.

According Freeze and Cherry's (1971) data, the saturation indexes for quartz have positive values (Fig. 2), both for *salinas* and *baías* samples (except for three *baías* samples), indicating that the mineral is mostly not dissolved. This observation is apparently discordant with the hypothesis that the geochemical erosion of quartz in *salinas* would explain their lower altitudes relative to these from hyposaline lakes, although the quartz dissolution may occur in physicochemical conditions not sampled in the survey, as solutions that precipitate amorphous silica in the sand of the *salinas* bottom. Furthermore, the adopted model explains the data for all the various types of observations made in the study. These include the relative altitude of the saline and hyposaline lakes, the ratios of stable isotopes of O and H, the differences in salinity and the origin of the silica in solution and, in images from scanning elec-

tron microscopy of the sediments below salinas, amorphous silica in the inter-grain spaces of the sediments under saline-alkaline lakes, corrosion figures at quartz grains and irregular grains surfaces in perfectly adjusted contact to each other. The authors have no alternative model to explain all the data from seven years of research in the region.

CONCLUSION

This paper presents an original interpretation of the origin of the diversity of Nhecolândia lakes, based on both geochemical and biogenic processes. The poverty in Ca^{2+} in the regional waters determines an imbalance of the calcium cycle, because this ion is responsible for maintaining the neutral pH of most surface water on Earth. We propose that this geochemical process was the first to increase the alkalinity of these lakes, according to a shift in the balance in the system $CO_2/ HCO_3^-/ CO_3^{2-}$ to CO_3^{2-} because of the inability to precipitate $CaCO_3$. The phytoplankton, mainly cyanobacteria, help to raise the pH by consuming inorganic carbon in the form of CO_2 and, markedly, HCO_3^- (which predominates in the solution from pH > 6), and by excreting OH^-.

Originally the water in the lakes should have been fresh, lacking a basis for high salinity. During the evolution of these lakes, the biogeochemical process raised the pH of the water, facilitating the dissolution of quartzose sand and silt. The silica-rich water (possibly as H_4SiO_4) penetrated the sediments below the lake bottoms, where amorphous silica was precipitated between

the clasts. This precipitation could be caused by excessive salinity (during extreme droughts) or drops in pH (due to contact with the water table). The repetition of this process, including the dissolution of the fraction of amorphous silica precipitated at the surface and of additional amounts of quartz (sand and silt), gradually increases the isolation of the lakes due to the precipitation of amorphous silica, which acts as a cement between the grains of sand, allowing the generation of high-salinity waters. Note that this repeated process will lead to a progressive lowering of the bed of the saline-alkaline lakes. The limit for this lowering may be the groundwater level in extreme drought, which explains the horizontal bottom of the saline-alkaline lakes.

RESUMO

O Pantanal da Nhecolândia é o maior e mais diversificado campo de lagos da região tropical do planeta, com cerca de 10.000 lagos de variadas salinidade, pH, alcalinidade, cor, fisiografia e atividade biológica dispostos em uma área de 24.000 km^2. Os lagos hipossalinos têm pH variável, baixa alcalinidade, macrófitas e baixa densidade de fitoplâncton. Os lagos salinos tem pH acima de 9 ou 10, elevada alcalinidade, alta densidade de fitoplâncton e praias de areia. A causa da diversidade desses lagos é uma questão ainda em aberto que é abordada nesta pesquisa. Propõe-se como principal causa um processo híbrido, geoquímico e biológico, baseado em (1) clima com um déficit hídrico importante e pobreza em Ca^{2+}na água superficial e do freático e (2) na elevação do pH durante florações de cianobactérias. Estes dois aspectos desestabilizam a tendência geral de pH neutro para as águas superficiais da Terra. Este desequilíbrio resulta em aumento do pH e dissolução da areia quartzosa do fundo dos lagos salino-alcalinos. Durante secas extremas há precipitação de sílica amorfa nos espaços inter-granulares dos sedimentos de fundo destes lagos, aumentando seu isolamento do freático. O artigo discute este processo biogeoquímico, à luz de dados físico-químicos, químicos, fitoplânctonicos e de altimetria de precisão.

Palavras-chave: Pantanal, lagos alcalinos, lagos salinos, cianobactérias, processos de alcalinização.

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