Nutrients and water-forest interactions in an Amazon floodplain lake: an ecological approach

Nutrientes e interações aquático-florestais em um lago da planície amazônica: uma abordagem ecológica

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Abstract: Aim: Catalão Lake was surveyed between 2002 and 2011 with the aim of studying seasonality of the flow of nutrients between water, sediment and aquatic macrophytes. The role of the flood pulse and the ecological mechanisms influencing the forest-water interactions in the Amazon floodplain were discussed; **Methods:** Catalão Lake is located in the Amazon floodplain (03° 08'-03º 14' S and 59° 53'-59° 58' W), near the confluence of the Solimões and Negro rivers, approximately 3000 m from the port of CEASA, near the city of Manaus. It is considered to be a mixed water lake because it receives white waters rich in sediments from the Solimões River and black waters with humic substances from the Negro River. Physical and chemical parameters including C, N and P levels were studied in the diverse compartments, and a flux model was developed; **Results:** There is a strong nutritional (C, N and P) and ionic (Na^+, K^+, Ca^{2+}, Mg^{2+}, Cl^-, HCO^{3-}, CO_3^{2-} and SO_4^{2-}) flow from the rivers to the lake. The highest C:N:P ratio was found in *Paspalum repens* which, during periods of drought, played an important role in releaseing nutrients into the water. The connectivity of the lake with the rivers ensured a high variation of transparency and nutrient content, fundamental for biological processes. A model of the nutrient flow, interaction and connectivity between ecosystems, and the influence of the hydrological cycle has been developed.

Keywords: carbon, nitrogen, phosphorus, connectivity, Amazonian mixed lake.

Resumo: Objetivo: O lago Catalão foi pesquisado entre 2002 e 2011 com o objetivo de estudar sazonalmente o fluxo de nutrientes entre os compartimentos água, sedimento e macrófitas aquáticas. O papel do pulso de inundação e os mecanismos ecológicos que influenciam a interação aquático-florestal na planície amazônica foram discutidos; **Métodos:** O lago Catalão está localizado na planície amazônica, próximo à confluência dos rios Solimões e Negro, aproximadamente 3000 m do porto da CEASA, próximo a cidade de Manaus. Ele é considerado um lago misto, que recebe águas brancas ricas em sedimentos do rio Solimões e águas pretas contendo substâncias húmicas do rio Negro. Parâmetros físicos e químicos incluindo teores de C, N e P foram estudados nos diversos compartimentos, e um modelo de fluxo foi desenvolvido; **Resultados:** Há um forte fluxo nutricional (C, N e P) e iônico (Na^+, K^+, Ca^{2+}, Mg^{2+}, Cl^-, HCO^{3-}, CO_3^{2-} e SO_4^{2-}) dos rios para o lago. Dentre as espécies de plantas mais abundantes a maior razão C:N:P foi encontrada na *Paspalum repens*, que durante os períodos de seca teve importante papel na liberação de nutrientes para a água, garantindo a manutenção da vida das espécies aquáticas. A conectividade do lago com os rios garantiu uma alta variação da transparência e teores de nutrientes, fundamentais nos processos biológicos. Um modelo de fluxo de nutrientes, interação e conectividade entre os ecossistemas, e a influência do ciclo hidrológico, foram desenvolvidos.

Palavras-chave: carbono, nitrogênio, fósforo, conectividade, lago misto da Amazônia.

1. Introduction

The wetlands of the floodplain areas can be defined as transition systems between aquatic and terrestrial ecosystems, where according to Junk (1983), various compartments are in constant interaction, influenced mainly by the flood pulse of the region. The sediments of wetlands are composed of slightly consolidated substrates, hydromorphic and poorly drained soils. Since the water column usually acquires the physical, chemical and physical-chemical properties of the predominant water mass in the system at any given time of the hydrological cycle. The wetlands are the habitat of various aquatic macrophytes, as well as other species of plants, invertebrates and fish. The aquatic macrophyte communities have an important role in the flow of nutrients within lake ecosystem, contributing significantly to the physical and biological diversity, habitat structure, nutrient storage and ecological functioning of the lakes (Junk and Howard-Williams, 1984; Piedade, 1988; Darwich, 1995; Baattrup-Pedersen et al., 2003; Baattrup-Pedersen and Riis, 2004; Cotton et al., 2006; Lacoul and Freedman, 2006; Pedersen et al., 2006).

The richness and abundance of species of macrophytes in the floodplain is unique. According to Gopal (1999), floodplains are among the most productive natural systems on earth and are vital for the conservation of biodiversity. Floodplains receive and redistribute the input of sediments containing nutrients important for the maintenance of life in the region. In the Amazon floodplain there are lakes, which undergo periodic changes in the volume of water and nutrient concentrations due to the influence of the flood pulse (Junk, 1997; notes of the authors). In general floodplain lakes are shallow and are connected to the main river at least once during the hydrological year. During the flood river water invades the lakes, which return to the river in the ebb. These exchanges of water cause periodic changes in the concentration of nutrients, energy flow, abundance and biodiversity in the aquatic ecosystem (Junk, 1983; Ferreira and Stohlgren, 1999; notes of the authors).

Catalão Lake is situated in this mosaic. It is a lake that is unique in mixed characteristics, having been chosen among many other lakes to study the flow of nutrients and water-forest interactions under an ecological approach in the region. Among many aspects that could be addressed in this study we attempted to answer the following questions: What is the influence of the flood pulse in mixed floodplain lakes of the Amazon? What are the main ecological processes and mechanisms of forest-water interaction in these lakes? For this, we identified the routes of flow of nutrients (C-N-P) and the seasonal ionic balance in the water, sediment and aquatic macrophytes compartments.

2. Material and Methods

2.1. Study area

Catalão Lake (03° 08'-03° 14' S and 59° 53' - 59° 58' W) is a fluvial-lacustrine system with several interconnected small lakes, formed by the floodplain and situated near the confluence of the Solimões River (white waters) and Negro River (black waters), approximately 3000 m from the port of CEASA, downstream from the city of Manaus (Figure 1). Despite its proximity to a major urban center it has a great biological diversity and is also an important ecotone, serving as a spawning site and a migratory route of fish (Goulding, 1980; Araújo-Lima, 1984; Lima and Araújo-Lima, 2004). The Catalão Lake is part of a typical floodplain system, caused by sedimentation processes arising from the transgression and regression of the Amazon River, about 75,000 years ago (Sioli, 1984). The climate is warm and humid with average temperatures in the range of 26.6 °C, with warmer months between August and November. The relative humidity reaches its maximum in April (86.7%) and minimum in September (75.5%; Darwich, 1995). The predominant vegetation is riverine forest subject to seasonal flooding (flooded forest), particularly abundant along the edges of the relatively high and steep valleys of the streams and adjacent side arms, with altitudes around 12 meters, just above the flood pulse of Negro and Solimões rivers. An important aspect of the local vegetation is the formation of numerous stands of macrophytes, which reach maximum expansion at the end of the flood and the beginning of the flood-peck. Great stands of floating and rooted macrophytes proliferate during this time, covering approximately 25% to 50% of the pelagic region of the lake. Depending on the stage of the river, the maximum depth of the lake ranges from 1 to 14 meters (Darwich, 1995; Ferreira and Stohlgren, 1999; notes of the authors). The environmental complexity of the Catalão Lake is caused by the meeting of white and black waters. The Catalão Lake is an interesting place, in all respects, for scientific research.

2.2. Analytical procedures

From 2002 to 2011 waters were collected during flooding, flood-peck, ebb and drought periods at six sampling stations in Catalão Lake (Figure 1),

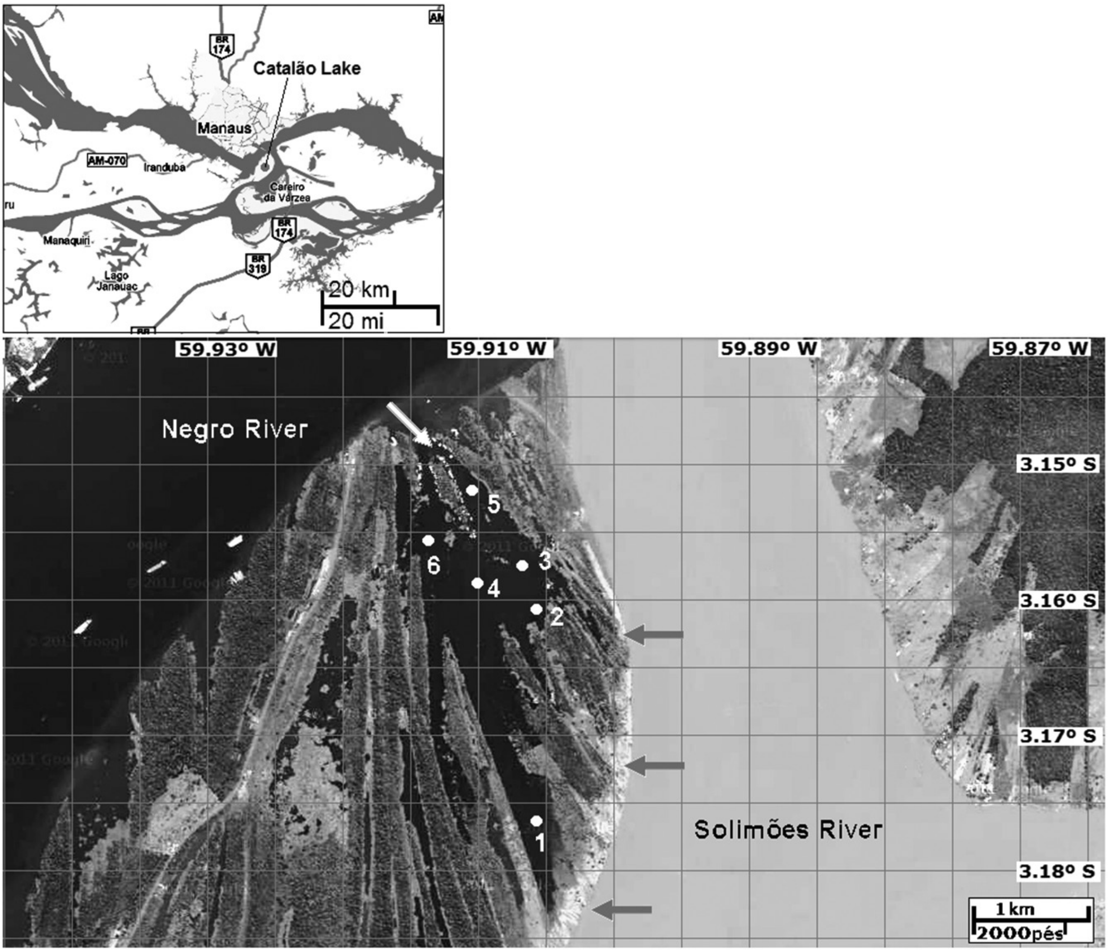

Figure 1. Location of the Catalão Lake basin, near the meeting of the waters of the Solimões and Negro rivers, with the sampling stations, indicating the major pathways of water flow and sediment to the lake.

summarizing 128 samples. Depth (m), water temperature (°C), percentage of oxygen saturation (% O_2), pH and electrical conductivity (EC $\mu S_{25}.cm^{-1}$) were measured at intervals of 0.5 meters from surface to bottom with a thermistor and digital oximeter WTW model OXI-197. Samples of water (*w*) were collected with Ruttner bottle, sediments (*s*) were collected with a Ekmann model dredge and aquatic macrophytes (*m*) were manually collected at six stations, and were used for analysis of total carbon (TC), total inorganic carbon (TIC), organic carbon total (TOC), total nitrogen (TN), total inorganic nitrogen (TIN), total organic nitrogen (TON) and total phosphorus (TP), all expressed as [*w*] $mg.L^{-1}$, and [*s*] and [*m*] $mg.kg^{-1}$. Eight species of aquatic macrophytes in this study were selected for analysis of nutrient content: *Echynochloa polystachya* (Nees) Hitche, *Azolla caroliniana* Willd, *Eichhornia crassipes* (Mart.) Solms, *Ludwigia natans* (Ell.), *Paspalum repens* (Berg.), *Pistia stratiotes* (L.), *Pontederia rotundifolia* (L.) e *Salvinia auriculata* (Aubl.). After collecting the plants were washed with water from the lake and stored in plastic bags. In the Water Chemistry Laboratory at INPA the plants and sediments were dried at 50 °C to constant weight, crushed, pulverized and sieved through a 250 mm mesh size sieve. The data collection, storage and procedures followed international protocols described in Wetzel and Likens (2000) and APHA (2012).

The carbonated forms were obtained by analytical methods and equations described by Golterman et al. (1978), Grasshoff et al. (1983), Strickland and Parsons (1984) and Carmouze (1994). The free CO_2 (CO_{2F}) and total CO_2 (CO_{2T}) were obtained by potentiometric titration with NaOH (pH = 8.3) and HCl (pH = 4.3), being considered for CO_{2T} the consumption of HCl used in the titration (Equation 1). The difference between the concentration of CO_{2T} and CO_{2F} depended especially of temperature, initial pH of the sample, alkalinity of carbonate and of the ionic composition. Total alkalinity (TA) and the alkalinity of carbonate (AC) were obtained by calculation from the potentiometric titration in the analysis of CO_{2F} and CO_{2T} (Equations 2-4). The carbonate and bicarbonate were calculated from the values obtained of alkalinity. The production and removal of CO_2 resulting of photosynthesis and respiration, respectively, were analyzed by variations in the sum of all forms carbonated [$H_2CO_3 + HCO_3^- + CO_3^{2-}$] more the content of CO_{2F}, thus obtaining the TIC (Equation 5). For comparison of the results the TIC was obtained also by direct relation with the concentration of CO_{2T} by molar transformation (Equation 6). Chemical oxygen demand (COD) were determined using $KMnO_4$ as oxidizing agent, and from the result of the COD was calculated the TOC (Equation 7). TC represents the sum of TIC and TOC. TN was determined by digestion in an autoclave for 30 minutes with an oxidizing solution of $K_2S_2O_8$ and H_3BO_3, as recommended by Valderrama (1981). TON was determined by the classical Kjeldahl method modified by Aprile and Bianchini Junior (2003a), described for analysis of sediment and plants, which consists of three steps: acid digestion (H_2SO_4) with temperature control, followed by distillation with NaOH and H_3BO_3, and titration with H_2SO_4. TIN represents the difference between TN and TON, and PT was determined by the ascorbic acid method, with acid extraction (H_2SO_4 + HCl) followed by spectrophotometric reading at 725 nm, according to the method of Braga and Defelipo (1974) modified by Aprile and Bianchini Junior (2003b).

The ionic balance in the water (Na^+, K^+, Ca^{2+}, Mg^{2+}, Cl^-, HCO^{3-}, CO_3^{2-} and SO_4^{2-}) in $mg.L^{-1}$ was determined by atomic absorption spectrophotometry, as recommended by APHA (2012). A comparison of mean values for the six sampling stations was made with a ANOVA (one-way single-factor).

2.2.1.Equations

$$CO_{2T} = 8.8 \times [HCl] \quad (1)$$

(note of the authors)

$$TA = \left[\left(\frac{V_{HCl} \times N_{HCl}}{V_{sample} + V_{HCl}}\right) - \frac{1}{10^{pH}.fH^+}\right] \times K \times 10^3 \quad (2)$$

(Aprile, 2012)

where: K is the constant of correction obtained in the table, and 10^3 the conversion factor to $meq.L^{-1}$.

$$TA = \left(2.5 - 1250 \times \frac{1}{10^{pH}.fH^+}\right) \quad (3)$$

(Strickland and Parsons, 1984)

$$AC = TA - A \quad (4)$$

(Aprile, 2012)

where: A is the correction of the contribution of borate obtained in table ($meq.L^{-1}$).

$$TIC = CO_{2F} + H_2CO_3 + HCO_3^- + CO_3^{2-} \quad (5)$$

(Carmouze, 1994)

$$TIC = CO_{2T} \times K_1 \quad (6)$$

(note of the authors)

where: K_1 in this case is equivalent to 0.2729 or the molar ratio of 4C and 11O.

$$TOC = COD \times K_2 \quad (7)$$

(note of the authors)

where: K_2 this case is equivalent to 0.3754 or the molar ratio of C and O_2.

3. Results and Discussion

From the historical data of 2002-2011 was prepared a graph of variation of the hydrological cycle of the Catalão Lake and Solimões River (Figure 2), allowing the identification of the flood pulse on the area of floodplain. The low water period occurred between July and September, when Catalão Lake was shallow, around nine meters at the deepest station (station 5), and less than 1.5 meters at station 2. The Catalão Lake is considered a mixed lake because it receives waters from both the Negro River and Solimões River. There is also contribution of flow and reflux of black waters of the Negro River, especially in the area indicated in Figure 1, near sampling stations 5 and 6.

For the vast majority of lakes in the floodplain, the flood pulse is especially associated to the dynamics of the Solimões River. However, as mentioned the dynamics of water in the Catalão Lake also is influenced by the hydrological cycle of the Negro River. That fact can be confirmed by analyzing the horizontal gradient of pH, which ranged on average from 4.5 near the station 5 to 6.6 at station 1 (unpublished data). The mean amplitude of the Catalão Lake water level according to the hydrological cycle of the Solimões and Negro rivers is approximately 14 meters, with depths ranging between 7 and 20 meters during periods of drought and flood-peck, respectively (bars of gray color in Figure 2). It was found that the portions of the lake closer to the edges of the Solimões and Negro rivers have similar values of change of level, regardless of their maximum and minimum depths (note of the authors).

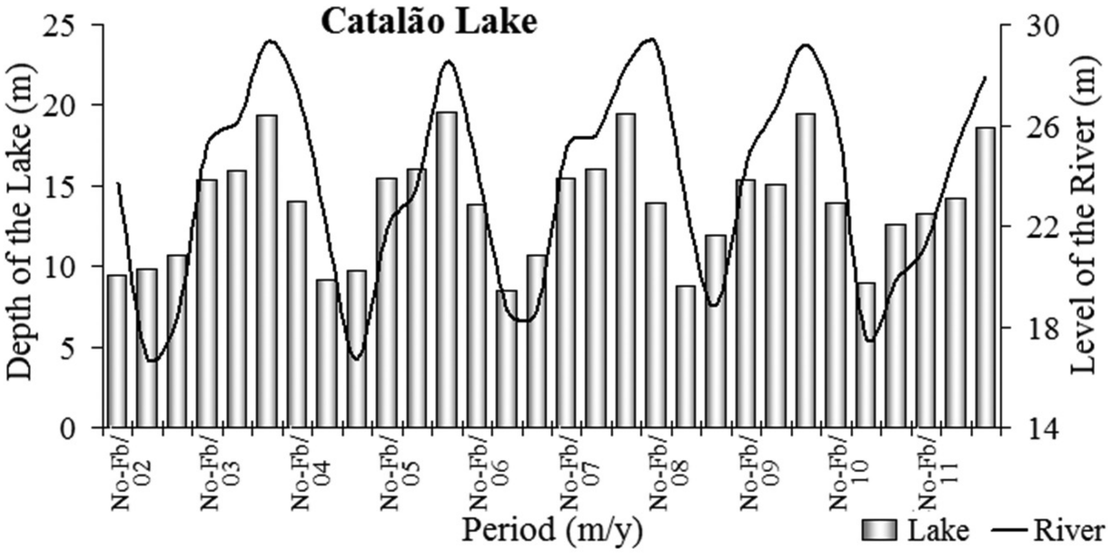

Figure 2. Lake depth and Solimões River hydrological level during the period of November 2001 to October 2011.

Lake depth can vary depending on the slope of the lake basin in relation to the river basin. That difference can be due to occasional or continuous depressions in the bed of the basin. The channel connecting Catalão Lake with the Solimões River is at a higher level, and as consequence the lake will always maintain a minimum depth limit, as much as the river level decreases along the hydrological cycle. One of the deepest stations of Catalão Lake, station 5, remains deep even during periods of drought, and consequently there is an accumulation of aquatic macrophytes in this section. The biological diversity of the lake is quite high, as has been observed over the ten years of research, and much of this is due to movement of white and black waters masses continuously throughout the hydrological cycle. Besides, Catalão Lake is fed by forest streams, a condition relatively common in the Amazonian lakes, allowing a steady flow of water from the lake to the river.

The vertical profile of temperature, oxygen saturation, pH and electrical conductivity are shown in Figure 3. An intense process of physical (thermal) and chemical (O_2) stratification was observed especially during the drought periods (Figures 3A and 3B). This condition shows that the Catalão Lake during the flooding has a complete or partially complete movement of water masses (Polymictic Lake), a behavior common in Amazon floodplain lakes (Esteves, 1998). Furthermore, the oxygen saturation curve shows that the lake has significant concentrations of gas throughout the water column during the flood-peck, as opposed to periods of drought when the lake below 2.5 meters is anoxic. It should be noted, however that the Catalão Lake as a shallow tropical ecosystem and that the dense population of aquatic macrophytes in the littoral region has significant daily variations in oxygen concentration. These variations occur mainly in the epilimnion in the flooding periods, when there is greater input of organic matter and suspended sediment (note of the authors). It was also noted by the authors that the range of variation of oxygen in the lake occurs mainly in the littoral zone in the period between dawn (3 am) and early morning.

The pH is significantly lower during the drought season (Figure 3C), which suggests that there is a greater influence in that period of the waters of the Negro River and the forest streams. This is because the black waters are naturally acidic (pH <4.5) by the presence of organic acids. However, when analyzing the comparative data for pH and EC, it is noted that it does not proceed, because at no time was there a predominance of black waters on white waters masses in the hydrological cycle, since the conductivity remained with values between 63 and 86 $\mu S_{25}.cm^{-1}$ (Figure 3D). The most plausible hypothesis is that with the drought are being aggravated the decomposition processes in the littoral zone, lowering the pH of the water column. The vertical profiles showed well the periods of flood-peck and drought showing that there is a physical and chemical difference between them.

The data show that the black waters that supply the Catalão Lake are acidic with low concentration of dissolved nutrients, resulting in a low EC (values between 8 and 20 $\mu S_{25}.cm^{-1}$, general data). In general, waters with a low content of mineral salts

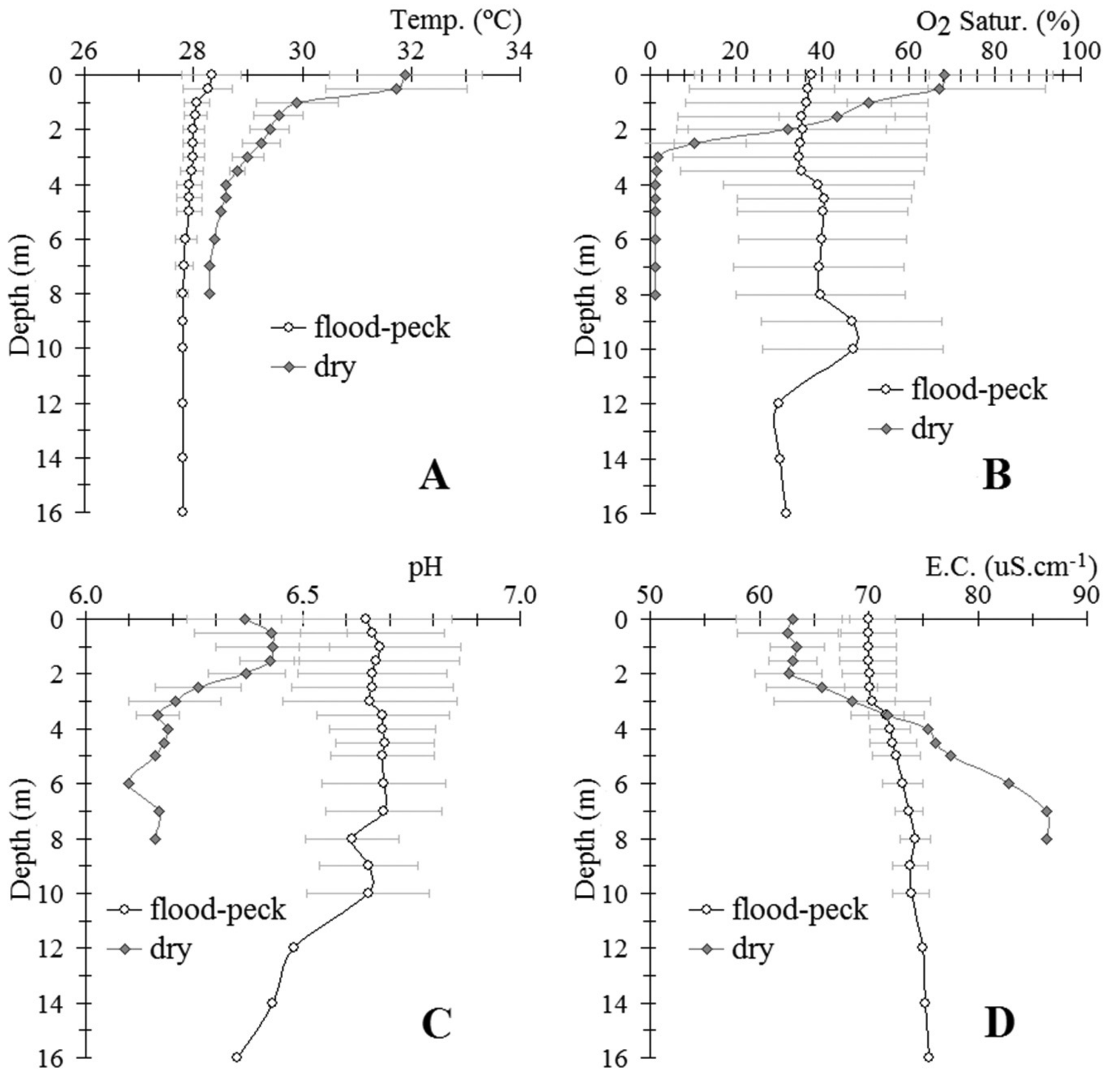

Figure 3. Vertical profile of limnological parameters for periods of flood-peck and drought of the hydrological cycle 2002-2011 in Catalão Lake - Central Amazon. Mean values with standard deviation.

show high levels of alkali metals, especially sodium (Na^+) and potassium (K^+) and low alkaline earth metals, especially calcium (Ca^{2+}) and magnesium (Mg^{2+}). The acidic condition of the black waters, due to the high concentration of humic substances, indicates that its buffering capacity is very low, so the pH can be influenced by the input and subsequent activity of the H^+ ion in the system. Therefore, the black waters can be characterized as "non-carbonated and not buffered waters." The white waters, responsible for most of the water supply in Catalão Lake, are relatively rich in nutrients (C, N and P) and mineral salts dissolved (Na^+, K^+, Ca^{2+} and Mg^{2+}; Darwich, 1995). The white waters have on average conductivity between 70-100 $\mu S_{25}.cm^{-1}$, and slightly acid to neutral pH, between 6 and 7 (note of the authors). The ionic concentrations of alkali metals, on average, varied according to the flood pulse (flooding, flood-peck, ebb and drought) between Na^+ = 1.5 and 3.2 $mg.L^{-1}$, K^+ = 0.9 and 2.0 $mg.L^{-1}$; Ca^{2+} = 4.7 and 8.8 $mg.L^{-1}$ and Mg^{2+} = 0.6 and 1.9 $mg.L^{-1}$. The ionic balance in the waters of Catalão Lake (Figure 4), heavily influenced by the white waters of the Solimões/Amazonas System, has a clear dominance of Ca^{2+} ions and bicarbonate (HCO_3^-), reflecting the lithology of the substrate of its catchment area of the "Piedmont Andino Peruano", which, according to Irion (1984) is characterized by the presence of carbonates. From a chemical standpoint, these waters can be considered a system of "carbonated water" characterized by relatively high content of electrolytes and strong dominance of Ca^{2+} and Mg^{2+} (Darwich, 1995). Although mixed with water from adjacent areas, the drainage basin of the Solimões River in the floodplain reflects more hydrochemical conditions of the pre-Andean area of the Central Amazon, where the lake is inserted.

The levels of total carbon in the water (TC_w) ranged between 28.7 and 37.6 mg.L^{-1} (average 31.6±4.1 mg.L^{-1} and p = 0.0652), and it was observed that the highest concentrations of this occurred during the drought periods. The main contribution of carbon in the water came from the organic form (TOC_w) than in the drought showed the highest levels 19.7 mg.L^{-1} (Figure 5A). In the sediment compartment the main contribution came from inorganic carbon (TIC_s), ranging between 21,400 and 32,700 mg.kg^{-1} (mean 25,825 ± 5518 mg.kg^{-1} and p = 0.4930, Figure 5C). In macrophytes the levels of total carbon (TC_m) ranged between 86,600 and 945,500 mg.kg^{-1} (Figure 5D) with p < 0.0001. The high standard deviation determined for the carbon in macrophytes indicates that the average in this case is not representative for the set of values. The total nitrogen in water (TN_w) ranged between 1.06 and 3.18 mg.L^{-1} with an average 2.02 ± 0.90 mg.L^{-1} and p= 0.0004. In water, the organic form of nitrogen (TON_w) was predominant on the inorganic form (TIN_w, Figure 5B). Total nitrogen levels in the sediment (TN_s) varied between 2340 and 3870 mg.kg^{-1} (average 3254 ± 649 mg.kg^{-1} and p = 0.0008), with higher concentrations of the inorganic fraction (Figure 5C), whereas the levels of total nitrogen in macrophytes (TN_m) were quite high compared to other compartments, ranging between 6,308 and 18,894 mg.kg^{-1} (mean 12,980 ± 6293 mg.kg^{-1} and p = 0.4772, Figure 5C). In the water, sediment and macrophytes compartments the total phosphorus levels ranged as follows: TP_w between 0.07 and 0.13 mg.L^{-1} (average 0.10 ± 0.02 mg.L^{-1} and p = 0.4981); TP_s between 19 and 52 mg.kg^{-1} (mean 40 ± 15 mg.kg^{-1} and p = 0.0489), and TP_m between 6 and 21 mg.kg^{-1} (mean 14 ± 7 mg.kg^{-1} and p = 0.4997; Figures 5A, B, respectively). It should be noted that the main reservoir of phosphorous was the sediment compartment (TP_s), while for carbon and nitrogen the largest reserves were found in macrophytes compartment (TC_m and TN_m).

Comparing the results of TC, TOC and TIC in the water [*w*] with sediment [*s*] and macrophytes [*m*], it can be verified that as the carbon content

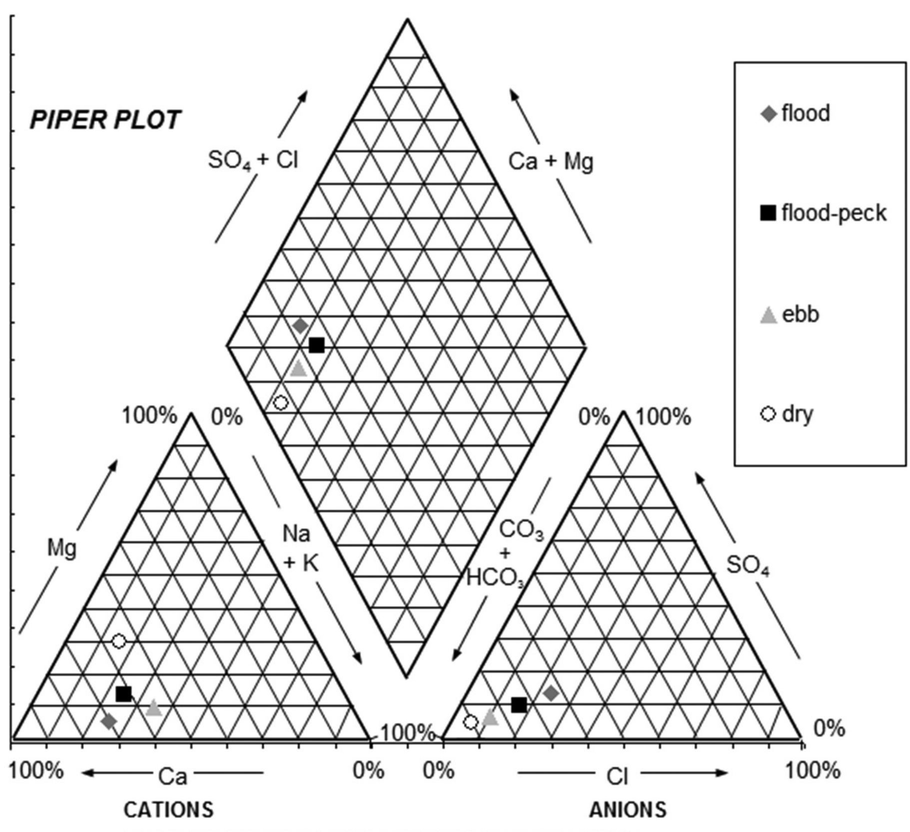

Figure 4. Ionic balance for the Catalão Lake's waters under the influence of Negro (black waters) and Solimões (white waters) rivers with data identifying the periods of the seasonal flood pulse.

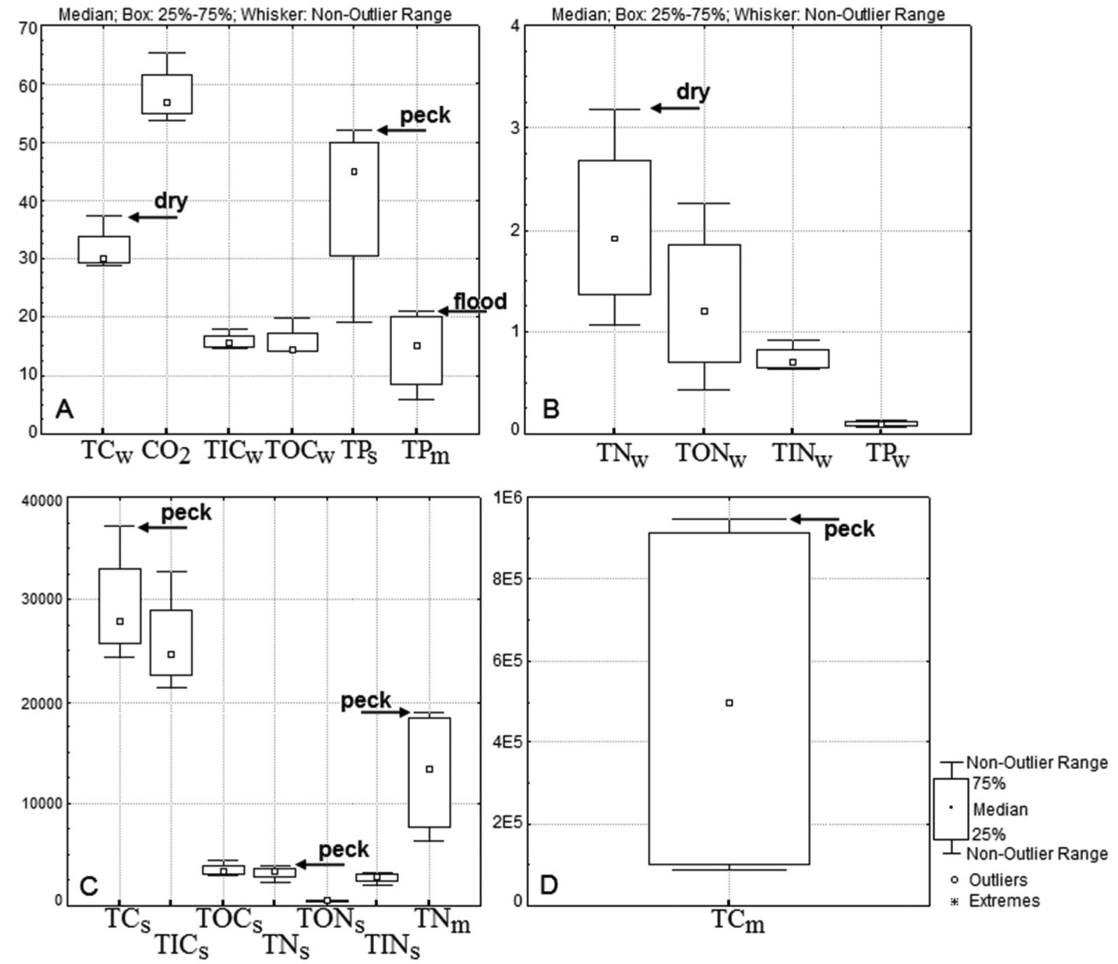

Figure 5. Boxplots for the compartments water (X_w), sediment (X_S) and macrophytes (X_M) indicating the maximum, medium and minimum of C, N and P in its various forms over the Catalão Lake.

in the water (TC_W) increased during the drought periods, an increase of 23.9% compared to flood periods, the concentration of TC_s and TC_m decreased in the respective compartments, with a mass reduction of 34.5% (TC_s) and 90.8% (TC_m). With the onset of the drought periods, the process of decomposition of aquatic macrophytes is accelerated, being observed in the field, releasing nutrients into the water column. In addition, during the drought the sediment compartment may still be stimulated to release nutrients into the water due to reduced oxygen concentration at the bottom of the lake (see Figure 3B). That trend was not just observed for carbon and its forms, but also for the nitrogen and phosphorus forms (Figure 5). Thus, it can be suggest that during drought periods the flow of nutrients (C, N and P) it is directed to the water column.

Most of the lakes of the Amazon have littoral regions colonized by different communities of aquatic macrophytes (Ferreira and Stohlgren, 1999; note of the authors). In the Catalão Lake the macrophytes species diversity is quite apparent. The authors believe that two factors are contributing to this high diversity: the sediment dynamics, which accounts for the supply of nutrients from the white water of the Solimões River, and humic substances brought by black waters of the Negro River. Moreover, the geomorphology of the floodplain promotes the continued flooding of the region, supporting even in drought periods many small wetlands inside the Catalão System, allowing the presence of macrophytes in the lake throughout the year. The percentage of dry weight of C, N and P for each species of macrophytes is shown in Figure 6. The results showed that among the most abundant species the largest ratio C:N:P was found

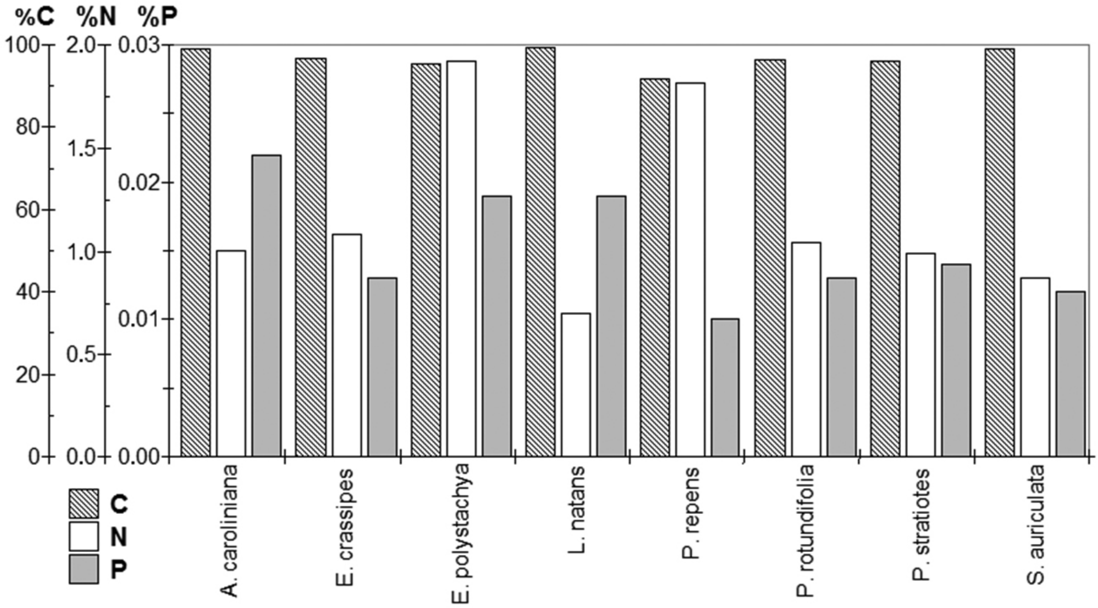

Figure 6. Percentage of dry weight of carbon, nitrogen and phosphorus in eight species of aquatic macrophytes found in the Catalão Lake, Central Amazonian.

in *Paspalum repens* 9169:180:1, and the lowest ratio in *Azolla caroliniana* 4494:45:1. *Paspalum repens* and *Echinochloa polystachya* are common on the stands of Amazonian lakes (Ferreira and Stohlgren, 1999; note of the authors). These species are usually the first major obstacle to the white waters rich in clay and minerals that come through the channel connection with the Solimões River, retaining most of the nutrients in the water through an efficient filtration system of solids. This trend was observed by the authors in other floodplain lakes located in the middle Solimões River (e.g. Arara Lake and Caapiranga Lake). In these lakes has been evident the gradual reducing of total solids in the connection channel in the direction from the river to the lake, a fact evidenced by increasing transparency and reducing the electrical conductivity (EC from 80 to 35 $\mu S_{25}.cm^{-1}$) in the same direction (unpublished data).

Amazonian floodplain lakes are supplied mainly by the rivers of white waters and can be formed both on islands and in the alluvial floodplains of the rivers. In the lakes located in the wetlands of the floodplain of the Amazon basin usually there are additional sources of clear waters and black waters coming from forest streams of the local drainage basin. Whatever the origin of the drainage basin, the floodplain lakes have one thing in common, the presence of one or more connection channels with the main river. However, the connection channel with the river is often not the main route of entry of water into the lake, since the floodplain that gives access to waters from river to lake in flood and flood-peck periods, is almost always much larger than the channel. Analyzing the results from the seasonal aspect, it is noted that during the flooding periods, the main contribution of nutrients and ionic elements to the water column of Catalão Lake came from the flooded soil, unlike the periods of drought, when the main source of nutrients was the decomposition of aquatic plants.

The density of aquatic macrophytes to be overcome, either floating or rooted, increases the efficiency of the filtration system, so that a large amount of the sediment load transported by rivers of white waters is retained in these plants, which respond by increasing its biomass, especially during high water periods (Ferreira and Stohlgren, 1999; note of the authors). The nutrient intake carried by the flood pulse begins to play an important role in increasing plant biomass of floating meadow. In the Catalão Lake, as in most lakes of the floodplain, the macrophytes grow abundantly from the channel to inland lake, in a consortium dominated in the littoral zone more externally by the species known as “grass” *E. polystachya* and *P. repens*, and more internally floating in the lake by *E. crassipes*, *P. stratiotes* and *S. auriculata* (note of the authors).

The degree of connectivity between the Catalão Lake and the Negro and Solimões rivers can influence the levels of suspended matter, transparency and nutrients, fundamentals in all the chemical processes triggered in the lake. Accordingly, turbidity, electrical conductivity and Ca^{2+} levels lower, progressively from the stations nearest to the Solimões River to the stations nearest to the Negro River. Thus, the input of nutrients and the chemical variation in the quality of lake waters are also related to the degree of connectivity to the river. The importance of these events varies seasonally in accordance with the phase of the hydrological cycle, and results in large variations in the nutrient load and sediment transported from the rivers to the lake (note of the authors).

The flooded areas, the channels and lake basins can serve as areas of deposition of sediments from the rivers. The sedimentation will be larger as larger the time so that the waters reach the lake, this because the deposition of particles occurs by gravity. Furthermore, the vegetation can reduce water flow and withhold dissolved ionic charge and particulate sediment.

3.1. Forest-water interactions in the floodplain: an ecological approach

To understand the interactions that occur between terrestrial and aquatic ecosystems requires knowledge of the geographical, geological, hydrological and hydrochemical characteristics of the region.

The interactions are complex, the rainforest can not survive without the river and the river can not survive without the forest. The cadence established for the fauna and flora that inhabit both the forest and the river is showed in the landscape that varies annually, influenced by the flood pulse. The hydrological regime in the Amazon River is annual and monomodal, just as the regime that controls the waters of the Catalão Lake (Figure 2).

According to Junk (1997), the flood pulse is the main driving force in flood plains of the Amazon. This force promotes various environmental changes, such as periodic alternations between fauna and flora communities, with biotic processes of production and decomposition of organic matter, sediment deposition and high species diversity. The connectivity between wetlands, channels, lakes and rivers has a gradient of direct and indirect interactions of great ecological and economic importance, with consequences for communities.

These large inland ecosystems with their natural variability of aquatic biodiversity, in association with the hydrological cycle, are now seen as "active centers of evolution" (Junk, 1983), establishing the connectivity of the system, promoting and encouraging biotic interactions and stimulating the local biodiversity in a dynamic way. The Catalão Lake as well as other lakes near the confluence of the Solimões and Negro rivers are important nursery grounds for fish and fish that spawn in the fluvial-lacustrine system of the Central Amazonian (Leite and Araújo-Lima, 2002; Leite et al., 2006). The richness of species, especially fishes, is explained in large part by the connection that exists between the black waters and white waters (Claro Junior et al., 2004), each with its particular physical and chemical properties, which supply the system with nutrients and creates a unique condition, the condition of mixed waters. The pattern of connectivity and the forest-water interactions are almost unique in the Amazon, since the Catalão Lake is one of the few lake systems of connection between white and black waters.

Biogeochemical cycles are quite efficient and very well versed with the local hydrological cycle. The trees remove from the soil all organic matter therein, leaving only a thin layer of humus, which guarantee the decomposers recycling nutrients. The removal of these minerals is so intense that some Amazonian rivers have their water almost distilled. In fact, in streams and rivers of black waters, most species of fish feeds on allochthonous material derived from the forest, such as fruits, seeds, leaves, insects and fungi (Junk, 1983; Waldhoff et al., 1996). The food webs in forest streams are based especially in terrestrial material. Most aquatic animals living of the forest, taking advantage of the large amount of plant material that falls into the water (Sioli, 1984; Junk, 1983; note of the authors).

For recycling of nutrients to occur there must be a large number of terrestrial and aquatic plant species, as each plays a role in the ecosystem. The relationship between the forest that borders the Catalão Lake and the allochthonous supply of nutrients reaching the water column is enhanced with the coming of the rains. The rains in tropical forests have an even greater role than simply supply the soil, surface water and ground water (recharge), they promote the circulation of nutrients from the leaves and trunks of trees, from the ground into water (Salati, 1983). The phenomenon of leaching is very important to lakes located inside the forest, ensuring the supply of several nutrients, particularly carbon, to the lake. The system is then considered in equilibrium when the forces flow to stabilize and each compartment has its role properly configured within the system (Figure 7). The constant rains in the study area are fundamental to the maintenance of the ecosystem. Often the water will not even reach the ground as it is retained in the various layers of vegetation, and is rapidly absorbed or evaporates at the end of the rain (Salati, 1983). Figure 7 presents a general model of the flow process of nutrients to the ecosystems of the Amazon floodplain based on studies carried out on the Catalão Lake.

The lowland forests have a different dynamic of upland forests, marshy, and forest streams of black waters. The floodplain is annually inundated with very fertile sediment (silt-clay), from the Andean and Pre-Andean regions as well as alluvial soils, which will fertilize the surrounding forest. The water of the Solimões River is rich in dissolved minerals and with the rise of the river water enters the channels and lakes in the floodplain, enriching them completely during the flood and flood-peck. Fluctuations in water level have an important function of driving force in the ecological functioning of ecosystems related (Ferreira and Stohlgren, 1999; note of the authors). The rivers and floodplains of the Solimões River are a complex of channels, rivers, lakes, islands and depressions, permanently changed by the transport and sedimentation of suspended solids, also influencing the succession of terrestrial vegetation by the constant modification, removal and sedimentation of material in the soil. The soil receives a supply of nutrients to be quickly incorporated into the plant biomass during the transition between ebb and drought periods. The time is short before a new flooding begins, therefore, the species that follow have little time to germination, nutrient uptake, flowering and fruiting. The same occurs during periods of ebb and flooding to the wetlands, where fish and various aquatic invertebrates have little time to grow and reproduce in the lakes and channels. The dynamics in the system increases with the flooding of the floodplain, and thus ensures the intense inflow of nutrients to the diverse parts of the lake.

The vegetation surrounding the Catalão Lake is composed of wetland forests and aquatic macrophytes in the lake and connecting channels, providing food and shelter for aquatic and terrestrial life. The highest areas of the floodplain are covered by trees that can withstand flooding for months. The trees start to sprout in the ebb and drought periods, and flower and fruit in the flooding. This is an example of an important ecological interaction, because fish are dispersing agents of the seeds (Junk, 1983; Kubitzki and Ziburski, 1994; Waldhoff et al., 1996; note of the authors), which ensures a greater chance of germination of seedlings away from the competition with the mother tree. The animals are also well adapted to the system of flood pulse. Various aquatic animals migrate from lakes to rivers and channels during the ebb, taking seeds and spores in the digestive tract to spread elsewhere (Junk, 1983; Kubitzki and Ziburski, 1994). Similarly, in the flooding and flood-peck, many terrestrial animals migrate to higher ground to escape the waters and also carry seeds with them.

Aquatic plants existing in the Catalão Lake have a strong plant-animal interaction. In the flooding the aquatic macrophytes floating, rooted and submerged form large stands in the lakes and channels, serving as a shelter for young fish of various species, insect larvae and other invertebrates (Araújo-Lima, 1984; Sánchez-Botero and Araújo-Lima, 2001; Schiesari et al., 2003), as well as serving

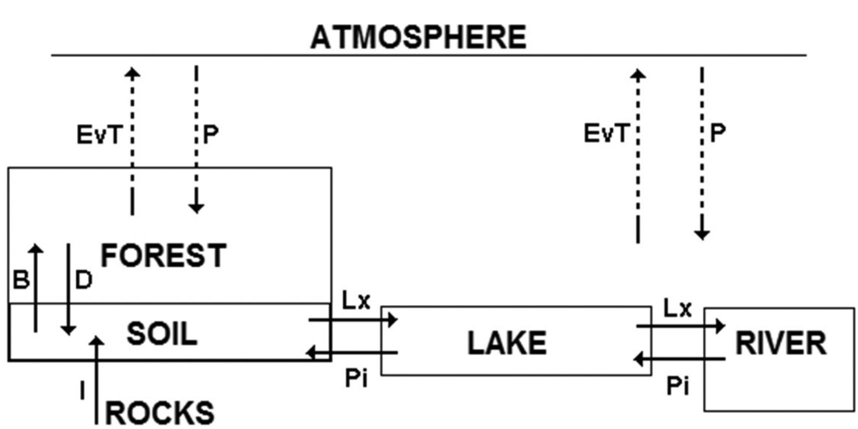

Figure 7. Inputs and outputs model of elements in Amazonian ecosystems of wetlands. EVT = evapotranspiration; P = precipitation; B = incorporation of nutrients into biomass; D = decomposition; I = weathering; Lx = leaching and erosion; Pi = flood pulse carrying nutrient-rich sediment.

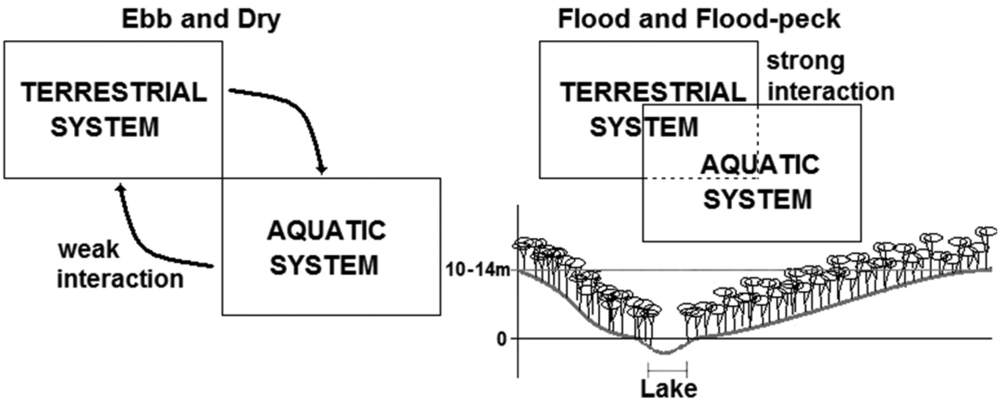

Figure 8. Degree of interaction and connectivity between terrestrial ecosystems and Catalão Lake as a function of the hydrological cycle.

as a point of rest for birds and reptiles. They follow the water level, getting the maximum possible exposure to light to develop photosynthetic activity. Some stands are so big they can be seen on satellite images and vegetation in the middle of the stream. In the ebb and drought most of the macrophytes decompose serving as the first source of organic compounds to aquatic organisms, and then the terrestrial plants start the germination from seeds that were dormant in the water.

There is a strong relationship of co-dependency between the forest and wetland forest, and in that sense it is possible to divide the processes of interaction in two major groups: 1) those that occur during periods of low water (ebb and drought) and 2) those that occur during periods of high water (flooding and flood-peck). During low waters the interaction between terrestrial ecosystems and Catalão Lake is less, and each ecosystem tends to maintain its dynamic equilibrium with their own resources obtained when there is a predominance of autochthonous processes. Already during the phases of high waters the interaction is strong (Figure 8), enriching the soil by the sediment brought down by the waters and distribution of food to aquatic organisms from forest products. At this time there is a predominance of allochthonous processes.

The classification of Amazonian waters reflects the differences between chemically rich alluvial waters from elevated areas of recent geological origin (white waters), and those with low suspended load and nutritional content from areas of low relief and geologically old (black waters). Transitions between these types can occur in spatiotemporal scale, due to the mixing of different volumes of water and seasonal changes in its load in suspension. This is the case of the Catalão Lake, which over a hydrological cycle shows a wide variation in the volume of white and black waters that are mixed, creating a variety of limnological trends. All the elements, climate, soil, flora and fauna are closely related, and the absence of any one of them is sufficient to cause the imbalance of the ecosystem. The flood pulse, seasonal phenomenon in the Amazon, ensures biological diversity in floodplain lakes, and for the authors in the Catalão Lake, for the fact of this to be a lake connected to two different fluvial systems (Negro River and Solimões River), the biological answer to the flow of nutrients is still larger.

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References

American Public Health Association - APHA, American Water Works Association - AWWA and Water Environment Federation - WEF. 2012. *Standard Methods for the Examination of Water & Wastewater*. 22nd ed. APHA/AWWA/WEF. 1496 p.

APRILE, FM. 2012. *Study of dynamics and mass balance model of carbon in estuarine system*. Saarbrücken: Lambert Academic Publishing. p. 103-104.

APRILE, FM. and BIANCHINI JUNIOR, I. 2003a. Adequação metodológica para determinação de Nitrogênio Orgânico Total em macrófitas aquáticas e sedimentos. *Revista Brasileira de Biociências*, vol. 8, p. 49-56.

APRILE, FM., BIANCHINI JUNIOR, I. 2003b. Adequação metodológica para determinação de

Fósforo Total em macrófitas aquáticas e sedimentos. *Revista Brasileira de Biociências*, vol. 8, p. 57-64.

ARAÚJO-LIMA, CARM. 1984. *Distribuição espacial e temporal de larvas de Characiformes em um setor do rio Solimões/Amazonas próximo a Manaus, AM*. Manaus: INPA. 84 p. [Dissertação de Mestrado].

BAATTRUP-PEDERSEN, A. and RIIS, T. 2004. Impacts of different weed cutting practices on macrophyte species diversity and composition in a Danish stream. *River Research Applied*, vol. 20, p. 103-114. http://dx.doi.org/10.1002/rra.722

BAATTRUP-PEDERSEN, A., LARSEN, SE. and RIIS, T. 2003. Composition and richness of macrophyte communities in small Danish streams - influence of environmental factors and weed cutting. *Hydrobiologia*, vol. 495, p. 171-179. http://dx.doi.org/10.1023/A:1025442017837

BRAGA, JM. and DEFELIPO, BV. 1974. Determinação espectrofotométrica de fósforo em extratos de solos e plantas. *Ceres*, vol. 113, p. 73-85.

CARMOUZE, JP. 1994. *O metabolismo dos ecossistemas aquáticos*: Fundamentos teóricos, métodos de estudo e análises químicas. São Paulo: Edgard Blucher Ltda/ FAPESP. 254 p.

CLARO JUNIOR, L., FERREIRA, E., ZUANON, J. and ARAUJOLIMA, C. 2004. O efeito da floresta alagada na alimentação de três espécies de peixes onívoros em lagos de várzea da Amazônia Central, Brasil. *Acta Amazonica*, vol. 34, no. 1, p. 133-137. http://dx.doi.org/10.1590/S0044-59672004000100018

COTTON, JA., WHARTON, G., BASS, JAB., HEPPELL, CM. and WOTTON, RS. 2006. The effects of seasonal changes to in-stream vegetation cover on patterns of flow and accumulation of sediment. *Geomorphology*, vol. 77, p. 320-334. http://dx.doi.org/10.1016/j.geomorph.2006.01.010

DARWICH, AJ. 1995. *Processos de decomposição de Echinochloa polystachya* (H. B. K.) Hitchock (*Gramineae = Poaceae*), *capim semi-aquático da várzea amazônica*. Manaus: INPA. 327 p. [Tese de Doutorado].

ESTEVES, FA. 1998. *Fundamentos de limnologia*. 2. ed. Rio de Janeiro: Editora Interciência Ltda. 601 p.

FERREIRA, LV. and STOHLGREN, TJ. 1999. Effects of river level fluctuation on plant species richness, diversity, and distribution in a floodplain forest in Central Amazonia. *Oecologia*, vol. 120, no. 4, p. 582-587. http://dx.doi.org/10.1007/s004420050893

GOLTERMAN, HL., CLYMO, RS. and OHNSTAD, MA. 1978. *Methods for Physical and Chemical Analysis of Fresh Waters*. 2nd ed. Oxford: Blackwell Scientific. 213 p. IBP Handbook no. 8.

GOPAL, B. 1999. Natural and constructed wetlands for wastewater treatment: potentials and problems. *Water Science Technology*, vol. 40, no. 3, p. 27-35. http://dx.doi.org/10.1016/S0273-1223(99)00468-0

GOULDING, M. 1980. *The fishes and the forest*. Los Angeles: University of California Press. 200 p.

GRASSHOFF, K., EHRHARDT, M. and KREMLING, K. 1983. *Methods of seawater analysis*. New York: Verlag Chemie. 419 p.

IRION, G. 1984. Sedimentation and sediments of Amazonian rivers and evolution of the Amazonian landscape since Pliocene times. In SIOLI, H., ed. *The Amazon*: limnology and landscape ecology of a mighty tropical river and its basin. Dordrecht: Dr. W. Junk Publishers. p. 201-214. (Monographiae Biologicae, no. 56).

JUNK, WJ. 1983. As águas da Região Amazônica. In SALATI, E., JUNK, WJ., SHUBART, HOR. and OLIVEIRA, AE., eds. *Amazônia*: desenvolvimento, integração e ecologia. São Paulo: Brasiliense. p. 45-100.

JUNK, WJ., ed. 1997. *The Central Amazon Floodplain: Ecology of a Pulsing System*. Berlin-Heidelberg: Springer-Verlag. 520 p.

JUNK, WJ. and HOWARD-WILLIAMS, C. 1984. Ecology of aquatic macrophytes in Amazonia. In SIOLI, H., ed. *The Amazon*: Limnology and landscape ecology of a mighty tropical river and its basin. Dordrecht: W. Junk Publ. p. 269-293.

KUBITZKI, K. and ZIBURSKI, A. 1994. Seed dispersal in flood plain forests of Amazonia. *Biotropica*, vol. 26, no. 1, p. 30-43. http://dx.doi.org/10.2307/2389108

LACOUL, P. and FREEDMAN, B. 2006. Environmental influences on aquatic plants in freshwater ecosystems. *Environmental Reviews*, vol. 14, p. 89-136. http://dx.doi.org/10.1139/a06-001

LEITE, RG. and ARAÚJO-LIMA, CARM. 2002. Feeding of the *Brycon cephalus*, *Triportheus elongatus* and *Semaprochilodus insignis* (Osteichthyes, Characiformes) larvae in Solimões/Amazonas River and floodplain areas. *Acta Amazônica*, vol. 32, no. 3, p. 129-147.

LEITE, RG., SILVA, JVV. and FREITAS, CE. 2006. Abundância e distribuição das larvas de peixes no Lago Catalão e no encontro dos rios Solimões e Negro, Amazonas, Brasil. *Acta Amazônica*, vol. 36, no. 4, p. 557-562. http://dx.doi.org/10.1590/S0044-59672006000400018

LIMA, AC. and ARAÚJO-LIMA, CARM. 2004. The distribution of larval and juvenile fishes in Amazonian rivers of different nutrient status. *Freshwater Biology*, vol. 49, p. 1-14.

PEDERSEN, TCM., BAATTRUP-PEDERSEN, A. and MADSEN, TV. 2006. Effects of stream restoration and management on plant communities in lowland streams. *Freshwater Biology*, vol. 51, p. 161-79. http://dx.doi.org/10.1111/j.1365-2427.2005.01467.x

PIEDADE, MTF. 1988. *Biomassa, produtividade e atividade fotossintética de Echinochloa polystachya* (H. B. K.) Hitchcock *(Gramineae = Poaceae), capim semi-aquático da várzea amazônica*. Manaus: INPA. 154 p. [Tese de Doutorado].

SALATI, E. 1983. O clima atual depende da floresta. In SALATI, E., JUNK, WJ., SHUBART, HOR. and OLIVEIRA, AE., eds. *Amazônia*: desenvolvimento, integração e ecologia. São Paulo: Brasiliense. p. 1-44.

SÁNCHEZ-BOTERO, JI. and ARAÚJO-LIMA, CAM. 2001. As macrófitas aquáticas como berçário para a ictiofauna da várzea do rio Amazonas. *Acta Amazonica*, vol. 31, no. 3, p. 437-448.

SCHIESARI, L., ZUANON, JA., AZEVEDO-RAMOS, C., GARCIA, M., GORDO, M., MESSIAS, M. and VIEIRA, EM. 2003. Macrophyte rafts as dispersal vectors for fishes and amphibians in the lower Solimões River, Central Amazon. *Journal of Tropical Ecology*, vol. 19, p. 333-336. http://dx.doi.org/10.1017/S0266467403003365

SIOLI, H. 1984. Introduction: history of the discovery of the Amazon and of research of Amazonian waters and landscapes. In SIOLI, H., ed. *The Amazon:* limnology and landscape ecology of a mighty tropical river and its basin. Dordrecht: Dr. W. Junk Publishers. p. 1-13. (Monographiae Biologicae, no. 56).

STRICKLAND, JDH. and PARSONS, TR. 1984. A Practical Handbook of Seawater Analysis. *Bulletin. Fisheries Research Board of Canada*, vol. 167, 3rd edition, Ottawa: Queen's Printer, 311 p.

VALDERRAMA, GC. 1981. The simultaneous analysis of total nitrogen and total phosphorus in natural waters. *Marine Chemistry*, vol. 10, p. 109-112. http://dx.doi.org/10.1016/0304-4203(81)90027-X

WALDHOFF, D., SAINT-PAUL, U. and FURCH, B. 1996. Value of fruits and seeds from the floodplain forests of Central Amazonia as food resource for fish. *Ecotropica*, vol. 2, no. 2, p. 143-156.

WETZEL, RG. and LIKENS, GE. 2000. *Limnolgical analysis*. Philadelphia: W.B. Saunders Co. 357 p.

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