

Phosphorus, nitrogen, and carbon contents of macrophytes in lakes lateral to a tropical river (Paranapanema River, São Paulo, Brazil)

Conteúdos de fósforo, nitrogênio e carbono de macrófitas em lagoas laterais a um rio tropical (Rio Paranapanema, São Paulo, Brasil)

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Abstract: Aim: The aim of this paper was to determine the phosphorus, nitrogen, and carbon contents of aquatic macrophyte species during two periods of the year in the land-water transition zone of three lakes lateral to the Paranapanema River (São Paulo); **Methods:** Plants, water, and sediment were collected during two distinct periods (August 1998 and February 1999) in three transects perpendicular to littoral zones of the sampled sites. For the determination of the phosphorus, nitrogen and carbon contents of aquatic macrophyte species, aerial and submerged plant structures (leaves, roots, and stems) were used; **Results:** In Camargo Lake, which has a poor connection with the river during the dry period (August 1998), the highest nitrogen content was obtained for *Salvinia auriculata* Aublet, while the highest phosphorus content was observed for *Eichhornia azurea* (Swartz) Kunth. During the rainy season (February 1999), *Echinochloa polystachya* (H.B.K.) Hitch was the species with the highest phosphorus, nitrogen, and carbon contents. In Coqueiral Lake (a lake with great connectivity to the river), the highest phosphorus and nitrogen concentrations during the dry period were observed for *Cyperus esculentus* L. Similar carbon contents were found for both *C. esculentus* and *Eichhornia azurea*. During the rainy season, the species with the highest phosphorus and nitrogen concentrations were *E. polystachya*, *Ludwigia octovalvis* (Jacq.) P.H.Raven, and *Polygonum spectabile* Mart. Considering the plants recorded during the dry period in Cavalos Lake, which is isolated from the river, *Myriophyllum aquaticum* (Vellozo) Verdcourt was the species with the highest phosphorus and nitrogen concentrations. During the rainy period, *C. esculentus* and *E. azurea* had the highest nitrogen concentration. All the aquatic macrophyte species presented similar carbon contents. The highest phosphorus concentration was that of *C. esculentus*; **Conclusions:** The bottom of Camargo and Coqueiral Lakes (both with permanent connection with the river) and some sites of Cavalos (an isolated lake) can be considered similar. They were characterized by sediment with more phosphorus, organic matter, silt, and clay than other sites, which can affect the macro-nutrient content of macrophytes. In the isolated lake, the degradation of submerged plants at the land-water interface contributed to the nutrient pool of aquatic macrophytes after rainfall.

Keywords: phosphorus, nitrogen, content, macrophyte, tropical lakes.

Resumo: Objetivo: O objetivo deste trabalho foi determinar os conteúdos de fósforo, nitrogênio e carbono de espécies de macrófitas aquáticas em duas épocas do ano na zona de transição terra-água de três lagos laterais ao Rio Paranapanema (São Paulo); **Métodos:** Plantas, água e sedimento foram coletados durante dois períodos distintos (agosto 1998 e fevereiro de 1999) em três transecções perpendiculares à zona litoral dos locais amostrados. Para a determinação do conteúdo de fósforo, nitrogênio e carbono das espécies de macrófitas aquáticas, estruturas aéreas e submersas dos vegetais (folhas, raízes e caules) foram usadas; **Resultados:** Na Lagoa do Camargo, que tem baixa associação com o rio durante o período seco (agosto 1998), o conteúdo mais alto de fósforo e nitrogênio foi encontrado em *Salvinia auriculata* Aublet. Durante a estação chuvosa (fevereiro 1999), *Echinochloa polystachya* (H.B.K.) Hitch foi a espécie com os conteúdos mais elevados de fósforo, nitrogênio e de carbono. Na Lagoa do Coqueiral (um ambiente com grande conectividade com o rio), as mais altas concentrações de fósforo e de nitrogênio durante o período seco foram observadas em *Cyperus esculentus* L. Conteúdos similares de carbono foram encontrados em ambos, *C. esculentus* e *Eichhornia azurea* (Swartz) Kunth. Durante o período chuvoso, as espécies com as mais elevadas concentrações de fósforo e nitrogênio foram *E. polystachya*, *Ludwigia octovalis* (Jacq.) P.H.Raven e *Polygonum spectabile* Mart. Em relação às plantas coletadas durante o período seco na Lagoa dos Cavalos, que é isolada do rio, *Myriophyllum aquaticum* (Vellozo) Verdcourt foi a espécie com as mais altas concentrações de fósforo e nitrogênio. Todas as espécies de macrófitas aquáticas apresentaram concentrações similares de carbono. A mais alta concentração de fósforo foi registrada em *C. esculentus*; **Conclusões:** Os sedimentos das Lagoas Camargo e Coqueiral (ambas com associação permanente com o rio) e alguns locais de fundo da Lagoa dos Cavalos (um ambiente isolado do rio) podem ser considerados como similares. São caracterizados por apresentar mais fósforo, matéria orgânica, limo e argila no sedimento que nos demais locais, podendo afetar o conteúdo em macro-nutrientes das macrófitas. Na lagoa isolada, a degradação de plantas submersas na interface terra-água contribuiu para o estoque de nutrientes das macrófitas aquáticas.

Palavras-chave: fósforo, nitrogênio, conteúdo, macrófitas, lagos tropicais.

1. Introduction

Investigations into the role of macrophytes at the land-water interface are extremely important, since these plants are involved in various processes in the aquatic ecosystem.

Vegetation affects the chemistry of water in different kinds of aquatic environments. It constitutes a pool compartment of nutrients, is a component of herbivory and detritus food chains, and greatly contributes to organic matter production (Wetzel, 1990; Esteves, 1998).

Aquatic plants colonizing lentic and lotic borders are often used as bio-indicators of water quality and as filtering organisms of particulate matter, sediment, and nutrients in the improvement of water quality in polluted environments. They also influence sediment biogeochemistry (Esteves and Camargo, 1986; Carpenter and Lodge, 1986; Esteves, 1998; Pompeo et al., 1999; Thomaz and Bini, 1999; Bianchini Jr., 1999; Valitutto et al., 2006).

Research on the chemical composition of aquatic macrophytes is of great importance, because it informs about the capacity of storage of nutrients (Barbieri and Esteves, 1991), the availability for growth (Gerloff and Krombholz, 1966), and the

nutritional value of the plants (Henry-Silva and Camargo, 2006).

Assessing the nutrient pool in an aquatic macrophyte biomass is important to determine the nutrients' influence on the total balance in the environment.

Since macrophytes inhabit the borders of aquatic ecosystems, which are considered an ecotone, plants can change the nutrient pool in water and sediment through processes such as decomposition, lixiviation, excretion, and assimilation. According to Nielson (1993), an ecotone is a transition zone between adjacent ecological systems. Frontiers between the marginal region of lakes and reservoirs and the adjacent terrestrial zone are called lentic ecotones (Pieczynska, 1990). These ecotones have a great diversity of macrophytes.

To investigate the role and importance of macrophytes in aquatic ecosystems, it is necessary to consider the chemical composition of this community in relation to the local conditions (water and sediment), because vegetation is partially affected by seasonal changes.

The present investigation was carried out in the transition zone (water-land ecotone) of three lakes

lateral to a tropical river in an attempt to answer the questions: a) Does the chemical composition of macrophytes vary between lakes and seasons? b) Does the lake-river connectivity affect the chemical composition of plants?

2. Material and Methods

2.1. Study area

The selected study area was the lakes located in the mouth zone of the Paranapanema River into the Jurumirim Reservoir (São Paulo, Brazil). This site has a diversity of aquatic environments, being constituted by the river channel and lateral lakes with various kinds of connections with the river. Both lentic and lotic edges have a predominance of an emergent aquatic plant, *Echinochloa polystachya* (H.B.K.) Hitch. This gramineous plant has a vigorous stem up to 15 m long. It is rooted in the borders of aquatic ecosystems and protrudes towards open waters (Pompeo et al., 2001). Other macrophytes are also found in the transition zone of the Paranapanema River–Jurumirim Reservoir, such as *Salvinia auriculata* Aublet, *Utricularia* sp.

Linnaeus, *Azolla* sp., *Ludwigia octovalis* (Jacq.) P.H.Raven, *Pistia stratiotis* L., *Limnobium stoloniferum* (G. Mey.) Griseb., *Polygonum spectabile* Mart., *Scirpus cubensis* Poep & Kunth, *Habenaria edwalli* Cojn, *Eichhornia crassipes* (Mart.) Solms., and *E. azurea* (Swartz) Kunth. The dominant aquatic macrophytes on the river borders are usually emergent plants. In the permanently flooded sites, lateral to the main channel of the Paranapanema River, stands of *Myriophyllum aquaticum* (Vellozo) Verdcourt, a submerged aquatic macrophyte, can be observed (Pompeo, 1996).

Three sampling sites were selected in the mouth zone of the Paranapanema River into the Jurumirim Reservoir: a lake (Camargo Lake) permanently connected to the river with low water renewal; another lake (Coqueiral Lake) also permanently connected and with high water exchange with the river, and a third lake (Cavalos Lake), which is isolated from the river (Figure 1). Camargo and Coqueiral Lakes are both affected by water level variations (Moschini-Carlos et al., 1998; Henry, 2009) and are also subject to the operation regime of the Jurumirim Reservoir, due to alterations in

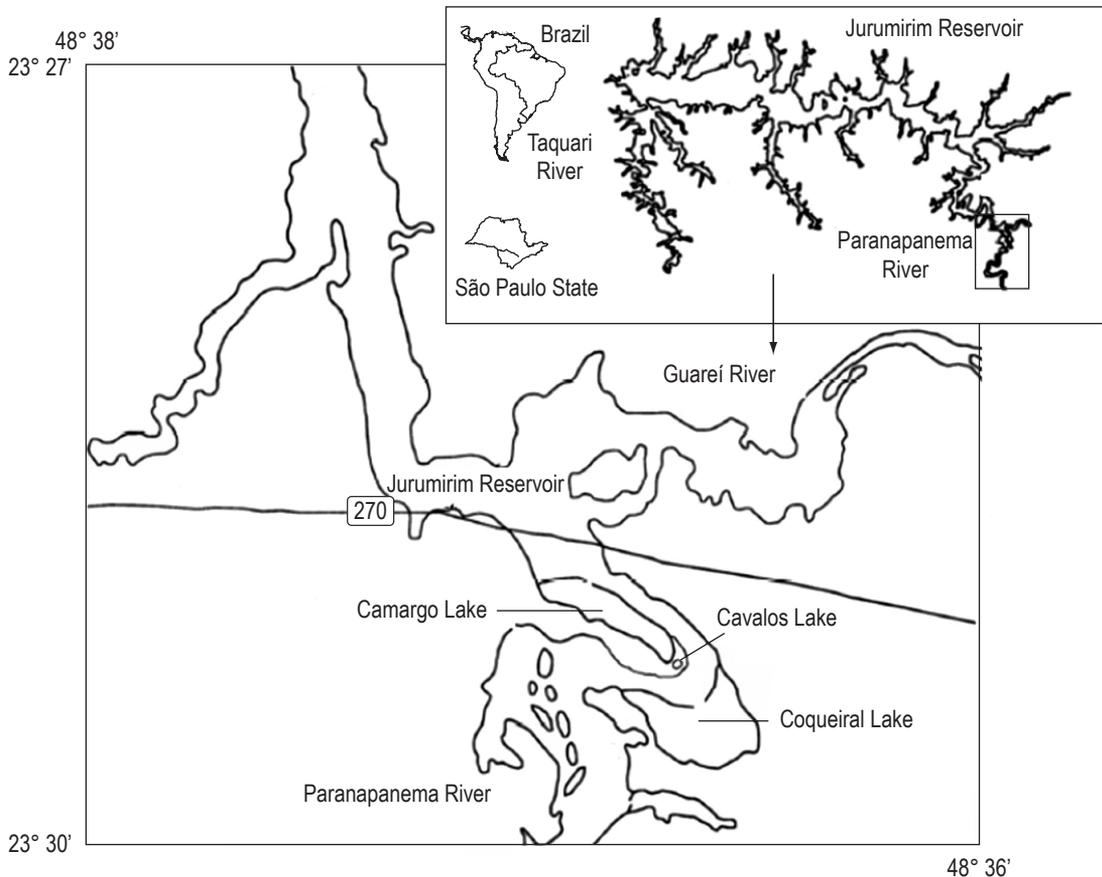


Figure 1. Study area and sampling sites.

water discharge to turbines. Thus, the variations of the hydrometric level of the reservoir affect the mouth zone of the main tributary, and consequently the floodable lateral aquatic environments (Costa and Henry, 2002).

2.2. Sampling procedure

Plants, water, and sediment were collected at three sites (in the terrestrial-littoral, intermediate, and littoral-limnetic zones) in three transects perpendicular to the lake shoreline in two periods, the dry (August 1998) and rainy (February 1999) seasons. Macrophytes were sampled in 0.25 m² quadrants (Westlake, 1965, 1971). The plants were carefully washed with water in the laboratory to remove adhered periphyton and organic and inorganic particulate matter. Next, the plants were oven dried (at 80 °C) to determine the biomass. The dry matter was ground and sieved through a 0.5 mm mesh net and stored in plastic flasks.

The phosphorus and nitrogen concentrations were determined in 0.3 g of macrophyte dry samples, according to Andersen (1976), and by the Kjeldahl method, using Buchi equipment, respectively. Carbon concentration corresponded to 47% of organic matter (Westlake, 1963), after burning 0.3 g of dry macrophyte mass for 1 h in an oven at 550 °C. Carbon, nitrogen, and phosphorus stocks were determined by multiplying their concentrations (in mg of element per g of dry weight) and biomasses (in g dry weight.m⁻²)

At each macrophyte sampling site, surface water was collected to determine dissolved oxygen (Golterman et al., 1978), pH (in a Micronal mod. B380 pHmeter), conductivity, corrected for 25 °C (in a Hach Mod. 2511 conductivimeter), suspended matter (by the gravimetric method, after water filtration in AP20 Millipore filters), alkalinity (after water acidification with 0.01 N HCl (MacKereth et al., 1978), total nitrogen (Valderrama, 1981), and phosphorus (Strickland and Parsons, 1969; Valderrama, 1981). Water Secchi disk transparency and depth were also measured at each site.

Sediment was sampled in all the sites by a Van Veen dredge. Granulometric composition was determined according to Suguio (1973). Organic matter in sediment was determined after sample burning (at 550 °C for 2 hours), and the ash content was obtained. The amount of organic matter in sediment (data transformed in %) was determined as the difference in weights before and after burning. Nitrogen in sediment, expressed in % of dry weight,

was measured using the Kjeldahl technique after acid digestion. The phosphorus concentrations in sediment samples were determined after acid digestion according to Andersen (1976) and Strickland and Parsons (1960) and were expressed as % of dry weight.

In order to assess significant differences ($p < 0.05$) between water and abiotic sediment variables of two seasons in the three lakes, an ANOVA was carried out using a 2 × 3 factorial design in an entirely casual procedure, followed by the Duncan comparison test (Gomes, 1990).

Sampling sites of the three transects (in three positions, three lakes, and two periods of the year) were arranged according to the sediment characteristics through a principal component analysis, after performing a correlation matrix of the variables nitrogen, phosphorus, organic matter, water content, sand, silt, and clay in sediment as discriminating variables after standardization (Manly, 1994; Hair Jr. et al., 1998).

3. Results

Water transparency, suspended matter, water content in sediment, and water pH showed no significant differences between lakes and year periods (Table 1). Widths of macrophyte stands, total phosphorus in water (only during the rainy period), and sand and clay in sediment presented significant differences only between lakes (Table 1). Depth and widths of macrophyte stands showed the lowest means in Cavalos Lake in relation to the other two lakes (Table 1). Water conductivity and alkalinity, and total nitrogen and phosphorus on the water surface were significantly higher during the rainy period in Cavalos Lake than in the other two lakes (Table 1). Total nitrogen and phosphorus, as well as organic matter, clay, and silt in sediment, had lower mean values in Cavalos Lake than in the other two aquatic ecosystems.

The ordination of sediment variables by principal component analysis showed that the first axis explained 65.1% of total data variability, while the second explained 14.2% (Table 2). In relation to the two principal components, the data were arranged in two groups (G): the first (G1), comprising all the sites of Camargo and Coqueiral Lakes and some of Cavalos Lake, was characterized by sediment presenting more phosphorus, organic matter, silt, and clay, while the second (G2), which included sites of Cavalos Lake and some of the Camargo Lake, presented sediment characterized by more sand and water content. Both ensembles

Table 1. ANOVA F values in the abiotic factors comparison between lakes and periods, and Duncan test of means parameters (values followed by the same letter are not significantly different; *p < 0.05 for F values).

Variables	F values		Variable/ period	Duncan test values		
	Lake	Period		Camargo Lake	Coqueiral Lake	Cavalos Lake
Depth	5.92*	10.21*	Depth	1.82 ^a	1.65 ^a	1.03 ^b
Stand width	5.80*	2.50	Stand width	13.5 ^b	27.40 ^a	1.50 ^b
Water transparency	0.27	0.81				
Suspended matter	1.36	2.35				
Electric conductivity	9.52*	6.84*	Electric conductivity/dry	57.50 ^b	64.10 ^a	46.20 ^c
			Electric conductivity/rainy	52.20 ^b	46.70 ^b	92.30 ^a
Alkalinity	54.40*	109.40*	Alkalinity/dry	0.44 ^a	0.43 ^a	0.28 ^b
			Alkalinity/rainy	0.37 ^b	0.36 ^b	0.85 ^a
Total nitrogen	32.00*	21.40*	Total nitrogen/rainy	286.80 ^b	214.10 ^b	754.70 ^a
Total phosphorus	35.40*	1.40	Total phosphorus/rainy	20.80 ^b	29.00 ^b	95.90 ^a
Total nitrogen in sediment	7.22*	18.6*	Total nitrogen in sediment	0.61 ^a	0.67 ^a	0.31 ^b
Total phosphorus in sediment	19.6*	28.1*	Total phosphorus in sediment	0.04 ^b	0.05 ^a	0.01 ^c
% sand	12.9*	0.23	% sand	19.3 ^b	6.49 ^c	50.4 ^a
% clay	32.2*	11.6*	% clay	40.7 ^b	51.4 ^a	12.3 ^c
% silt	14.2*	1.48	% silt	34.1 ^a	36.5 ^a	13.8 ^b
Organic matter in sediment	14.5*	15.1*	Organic matter in sediment	12.5 ^b	18.1 ^a	4.45 ^c
Dissolved oxygen	9.33*	119.40*	Dissolved oxygen/rainy	4.73 ^a	4.63 ^a	1.51 ^b
% water content in sediment	1.10	0.56				
pH	0.19	3.44				

Table 2. Correlation of abiotic factor values with axis ordination of principal components (CP₁ and CP₂) and explained variances for each component (CP).

Variables	CP ₁	CP ₂
Nitrogen	-0.542	0.758*
Phosphorus	-0.771*	0.326
Sand	0.944*	0.276
Clay	-0.935*	-0.058
Silt	-0.751*	-0.480
Water content in sediment	0.855*	-0.020
Organic matter in sediment	-0.777*	-0.007
Explained variances (%)	65.1	14.2

* Significant when > 0.70.

presented a variation in sediment nitrogen content (indicated by CP₂), but it was higher in G1 than in G2 sites (Figure 2).

Table 3 presents the ranges (n = 9; three quadrants in each of three transects) of N, C, and P contents in aquatic macrophytes. The data show higher plant richness in the rainy season than in dry periods in Coqueiral and Cavalos Lake.

Comparing the means and the ranges of nitrogen and phosphorus contents in macrophytes in Camargo Lake, the values were higher in *Salvinia auriculata* than in *Cyperus esculentus* and *Eichhornia azurea* during the dry season. In relation to carbon, the highest mean and range were recorded for *E. azurea* (Table 3). In the rainy period, only two

macrophytes were found in the lake; of the two, *Echinochloa polystachya* showed higher means and ranges of carbon, nitrogen, and phosphorus contents than *E. azurea*.

In the dry period, a higher mean and range of nitrogen content was recorded for *Cyperus esculentus* than for *E. azurea* in Coqueiral Lake, but both species presented similar ranges of carbon and phosphorus contents. In the rainy season, the species with the highest means and ranges of nitrogen and phosphorus contents were *E. polystachya*, *Ludwigia octovalvis*, and *Polygonum spectabile* (Table 3).

In Cavalos Lake, *Myriophyllum aquaticum* presented a higher mean and range of nitrogen and phosphorus contents than *E. azurea* in the dry period, but similar carbon contents were observed. In the rainy season, the highest nitrogen contents were found for *Cyperus esculentus* and *E. azurea*, while *Cyperus esculentus* presented the highest phosphorus mean content and range. Comparison of the carbon content of these three plants in the rainy season revealed no difference (Table 3).

Considering all the studied macrophytes, higher nitrogen, phosphorus, and carbon stocks were found for *Eichhornia azurea* in both periods in the three selected lakes. In Cavalos Lake during the rainy period, however, *Brachiaria arrecta* (Hack. ex. Th. Dur. & Schinz) Stent. also presented high nutrient stocks (Table 4).

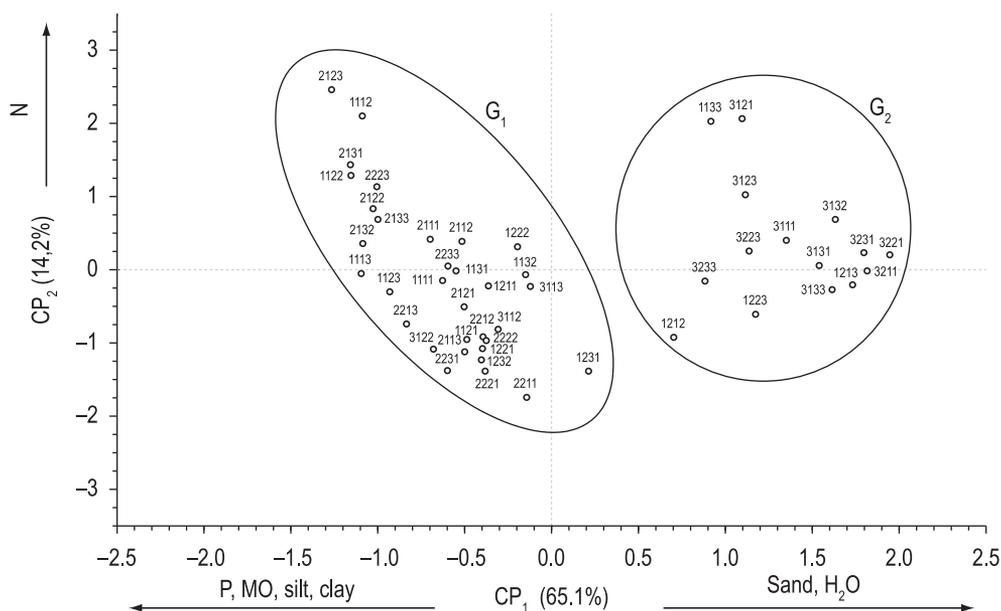


Figure 2. Sampling site arrangement according to principal components CP_1 and CP_2 . (The first number indicates Camargo (1), Coqueiral (2), and Cavalos (3). Lakes; the second, the dry (1) and rainy (2) sampling periods; the third, the transect (1, 2, and 3) and the fourth, the position in the transect, 1 limnetic – littoral, 2- intermediate, and 3, littoral – terrestrial zones; the arrows indicate the direction in which the original variables increase within each principal component; G1 and G2 are the groups shaped by the ordination analysis).

Table 3. Ranges (between parentheses) and means of nitrogen (N), carbon (C), and phosphorus (P) contents ($mg.gDW^{-1}$) of aquatic macrophytes sampled in Camargo, Coqueiral, and Cavalos Lakes in dry and rainy periods (n = number of sampled organisms).

Lake	Species/Taxa	n	Dry period			n	Rainy period		
			N	C	P		N	C	P
Camargo	<i>E. azurea</i>	9	(219-516) 391	(413-439) 430	(44-130) 76	6	(438-603) 506	(406-424) 418	(71-152) 110
	<i>C. esculentus</i>	6	(453-630) 567	(397-438) 416	(42-74) 57				
	<i>S. auriculata</i>	6	(606-618) 612	(376-378) 377	(63-78) 71				
	<i>E. polystachya</i>				3	(591-678) 647	(425-431) 432	(151-192) 234	
Coqueiral	<i>E. azurea</i>	8	(300-621) 393	(423-436) 431	(63-124) 86	7	(501-876) 685	(398-418) 409	(88-243) 160
	<i>C. esculentus</i>	6	(537-762) 612	(379-436) 414	(64-115) 88	1	627	388	87
	<i>E. polystachya</i>				1	1752	428	359	
	<i>L. octovalvis</i>				1	1239	389	501	
	<i>B. arrecta</i>				2	(480-762) 621	(409-433) 421	(80-208) 144	
	<i>P. spectabile</i>				1	1138	380	437	
Cavalos	<i>E. azurea</i>	8	(177-477) 313	(731-445) 437	(24-124) 78	6	(414-960) 623	(412-456) 425	(72-387) 178
	<i>C. esculentus</i>				4	(630-1020) 754	(402-434) 419	(92-966) 229	
	<i>B. arrecta</i>				3	(384-558) 449	(431-438) 434	(147-172) 163	
	<i>M. aquaticum</i>	7	(336-858) 490	(402-441) 430	(93-283) 161				

Table 4. Ranges (between parentheses) and means of nitrogen (N), carbon (C), and phosphorus (P) stocks ($\text{g}\cdot\text{m}^{-2}$) of aquatic macrophytes sampled in Camargo, Coqueiral, and Cavalos Lakes in dry and rainy periods (n = number of sampled organisms).

Lake	Species/Taxa	n	Dry period			n	Rainy period		
			N	C	P		N	C	P
Camargo	<i>E. azurea</i>	9	(4-244) 114	(59-805) 348	(9-203) 77	6	(71-149) 118	(228-384) 317	(47-139) 81
	<i>C. esculentus</i>	6	(5-60) 23	(11-147) 55	(1-19) 7				
	<i>S. auriculata</i>	2	(11-22) 17	(21-45) 33	(5-8) 6.5				
	<i>E. polystachya</i>					3	(44-107) 66	(99-221) 142	(38-123) 68
Coqueiral	<i>E. azurea</i>	8	(3-127) 64	(64-468) 234	(2-96) 46	7	(20-128) 74	(62-128) 179	(21-101) 68
	<i>C. esculentus</i>	6	(12-160) 52	(54-409) 167	(1-77) 33	1	12	24	5
	<i>E. polystachya</i>					1	53	84	72
	<i>L. octovalvis</i>					1	5	48	6
	<i>B. arrecta</i>					2	(7-8) 7.5	(13-22) 17.5	(4-7) 5.5
	<i>P. spectabile</i>					1	26	28	33
Cavalos	<i>E. azurea</i>	8	(9-140) 67	(76-691) 404	(7-200) 74	6	(13-128) 68	(19-338) 177	(17-130) 56
	<i>C. esculentus</i>					4	(9-21) 14	(13-42) 27	(4-15) 13
	<i>B. arrecta</i>						(56-168) 98	(176-256) 214	(70-96) 79
	<i>M. aquaticum</i>	6	(3-46) 22	(9-764) 183	(2-57) 24				

4. Discussion

Significant variations in nitrogen and phosphorus percentages were found in the sediment of the lakes between the two studied periods. Emergent aquatic macrophytes, such as *E. polystachya*, *Cyperus esculentus*, *Brachiaria arrecta*, and *Polygonum spectabile*, and rooted submerged plants, such as *Myriophyllum aquaticum* and *Ludwigia octovalvis*, had sediment as the main pool of nutrients. In the sampled sites with a predominance of emergent and submerged aquatic macrophytes, the concentration of phosphorus in sediment varied significantly. Coqueiral and Camargo Lakes presented higher amounts of clay, nitrogen, phosphorus, and organic matter in sediment in a decreasing order, while Camargo Lake had higher nitrogen and phosphorus contents in plants than the other two lentic ecosystems. In relation to the nitrogen content in sediment, Cavalos Lake showed a significantly lower content when compared with the other two lakes. Higher percentages of organic matter were found in sediment of Coqueiral Lake, and lower percentages in that of Cavalos Lake. Besides the input of

allochthonous matter to the lakes from the river, the increase in suspended matter sedimentation rates within the stands on the borders of the lakes and in the river channel can be attributed to the emergent rooted macrophytes, thus affecting the organic matter content at the bottom (Barko and Smart, 1980; Stephen et al., 1997; Cavenaghi et al., 2003; Henry, 2009).

Other sediment characteristics, such as geologic nature, granulometric composition, dissolved oxygen in interstitial water, and the amount of organic carbon, influence the nitrogen and phosphorus concentrations (Carr and Chambers, 1998). In Coqueiral Lake, the highest percentages of clay and silt, and the lowest amount of silt and dissolved oxygen were observed in sediment. As also observed was the highest diversity of aquatic plants and the highest nitrogen and phosphorus contents in their structures.

Free-floating macrophytes such as *Salvinia auriculata*, found only in Camargo Lake in the dry season, absorb nutrients from water. This taxon presented the highest nitrogen and phosphorus

contents when compared with the other two Camargo Lake macrophytes, *E. azurea* and *Cyperus esculentus*.

Spatial and temporal variations were evident in water-dissolved oxygen, electric conductivity, alkalinity, and total nitrogen and phosphorus (Costa and Henry, 2002). In Camargo and Coqueiral Lakes, both of which are connected to the Paranapanema River, the dissolved oxygen variation pattern was not significantly different in the rainy period. In contrast, Cavalos Lake, which is isolated from the river, showed a reduction in the dissolved oxygen content in the water. The rainfall and the underground inflow of water from the river to the lateral lake promoted an increase in the water level, submerging aquatic littoral and terrestrial plants (Carmo and Henry, in press). Degradation of submerged particulate organic matter produced a biochemical demand for oxygen, and dissolved oxygen concentration in the water decreased. After the decomposition of the organic matter, significantly higher alkalinity, and total nitrogen and phosphorus concentrations, were found in Cavalos, as compared to the other two lakes connected to the river (Costa and Henry, 2002). Loads introduced by the river into these two lakes during the rainy period produced no change in the total nitrogen and phosphorus concentrations in the water. However, evident spatial and temporal variations of alkalinity were observed in Camargo and Coqueiral Lakes. For electric conductivity, significant differences between lakes were limited to the dry season. The lowest conductivity was recorded for Cavalos Lake in the dry period (August), when the water temperature and decomposition rate were low. During the dry period, the mean electric conductivity of Coqueiral Lake was higher than that of Camargo Lake, which was probably due to the different patterns of inundation of the lakes, which increased ion release after plant decomposition. The conductivity of Camargo Lake in the rainy period presented a small reduction in relation to the dry season, which was probably due to a dilution effect of lateral water inflow from the Paranapanema River. This effect was well evidenced in Coqueiral Lake, an environment with great connectivity to the river (Costa and Henry, 2002). In a study of the relationship between water discharge and conductivity of Paranapanema River (sampled at approximately 60 km upstream from the mouth zone), Henry et al. (1999) showed a dilution effect of dissolved ions with the increase in water flow. The same was observed by Moschini-Carlos et al. (1998) for Camargo Lake, when a

great water volume is introduced during the rainy period.

Petrucio and Esteves (2000) studied the absorption rates of nitrogen and phosphorus by aquatic macrophytes *Eichhornia crassipes* and *Salvinia auriculata* and observed no increase in nutrient assimilation when high nitrogen and phosphorus concentrations were observed in water. According to these authors, *E. crassipes* absorbs nitrogen and phosphorus more efficiently than *Salvinia auriculata*. High concentrations of both elements cause a reduction in their assimilation rates from water by the two species.

The observed nitrogen and phosphorus concentrations of the studied macrophytes showed some differences between the plants. Some factors can be considered to explain the variations in the chemical composition of aquatic plants, such as trophic status of the lakes, physiognomy of the plants, and sediment characteristics.

In a study of the chemical composition of the main species of aquatic macrophytes in Recreio Lake in Pantanal, Mato Grosso (Brazil), Da Silva et al. (1993) observed that the phosphorus concentrations of *Eichhornia crassipes* and *Eichhornia azurea* were the lowest when compared with samples of the same plants from other water bodies. According to the authors, intra-specific variation can be related to different trophic conditions of each lake. Some studies indicate a relationship between nitrogen and phosphorus concentrations in water and in aquatic plants (Barbieri and Esteves, 1991; Nogueira et al., 1996; Petracco, 1997).

According to Gopal (1990), emergent aquatic macrophytes presenting more structural tissues usually have less nitrogen and phosphorus than floating and submerged species. The free-floating species *Salvinia auriculata* presented higher nitrogen concentrations during the dry period in Camargo Lake. However, in the rainy period, *E. polystachya* had the highest concentration of nitrogen, phosphorus, and carbon. Pompeo et al. (1999) investigated the chemical composition of *E. polystachya* in the transition zone of the Paranapanema River–Jurumirim Reservoir and found a seasonal concentration variation for nitrogen, phosphorus, and carbon, and substantial increases in February, a month before the flooding.

According to Lopes-Ferreira et al. (1998), most phosphorus retention depends on the frequency and duration of water level fluctuations and on the relative thickness of soils and the aerobic layer of sediment. Phosphorus is precipitated and stored

on the surface of sediment particles under aerobic conditions during the low water period and is released and absorbed under anaerobic conditions from the sediment or onto the soil surface immediately after flooding.

Species such as *E. azurea*, *E. polystachya*, *Cyperus esculentus*, *Brachiaria arrecta*, *Polygonum spectabile*, and *Ludwigia octovalvis* presented higher carbon concentrations when compared with *Salvinia auriculata*, a free-floating plant. Emergent aquatic macrophytes had a great amount of fibers because of their more developed support system, as compared with floating aquatic vegetation (Esteves, 1998). Emergent plants, therefore, must have a higher carbon concentration than floating plants, because this element is the main component of the plant support system.

Petracco (1995) reported that *Paspalum repens* and *Polygonum spectabile*, two emergent aquatic macrophyte species found in the Barra Bonita Reservoir (São Paulo, Brazil), presented high nitrogen and phosphorus concentrations. Similarly, in Coqueiral Lake during the rainy period, *Polygonum spectabile* and *Ludwigia octovalvis* were the two species with the highest nitrogen and phosphorus concentrations.

Myriophyllum aquaticum, a rooted submerged macrophyte from Cavalos Lake, presented nitrogen and phosphorus concentrations higher than *E. azurea* during the rainy period. Nogueira et al. (1996) found no temporal variation in nitrogen concentrations in the tissues of *E. azurea* sampled in Infernão Lake (São Paulo, Brazil). According to Ozimek et al. (1993), rooted submerged aquatic macrophytes absorb and store great amounts of nitrogen.

In rivers from the coastal plain of São Paulo (Brazil), Henry-Silva et al. (2001) found in free-floating macrophytes, stocks of N and P varying from 4.0 to 4.9 gN.m⁻² and from 0.5 to 1.2 gP.m⁻², respectively, which is around one order of magnitude lower than in plants of similar physiognomy in the lakes in the mouth zone of Paranapanema River into Jurumirim Reservoir. The discrepancy can probably be attributed to the high renewal of water in the coastal lotic ecosystems as compared with lentic environments, where an accumulation of macro-nutrients is a dominant characteristic.

Moraes (1999) studied the stock of chemical elements in four species of aquatic macrophytes (*Pistia stratiotes*, *Eichhornia crassipes*, *Brachiaria arrecta*, and *Cyperus sesquiflorus*) in the Salto Grande Reservoir (Americana, São Paulo) and observed that

Cyperus sesquiflorus showed a significant temporal range of nitrogen (from 1.62% in August to 2.45% in October). According to Moraes (1999), floating species compete with phytoplankton in the absorption of nutrient. This explanation can probably be applied to Cavalos Lake, where the highest nitrogen concentrations were found in *Cyperus esculentus*. In the rainy season, lake waters are very dark due to the decomposition of submersed organic matter after the rise in water level. In this condition, phytoplankton presented growth restriction due to limited radiation in this lake's water (Henry et al., 2006).

Temporal and spatial variations of aquatic macrophyte chemical composition in Camargo and Coqueiral Lakes appear to be related to the connectivity between the lakes and Paranapanema River. Camargo and Coqueiral Lakes are permanently connected to the river and present a high exchange of particulate matter and nutrients. Exchange affects the substrate heterogeneity, which is important for the presence of different ecological aquatic plant groups. In this study, predominance was observed for emergent macrophytes that had sediment as the most important nutrient pool. In Cavalos Lake, which is isolated from the river, rainfall appears to be an important controlling factor in the increase in water level, lake volume, and flooding of the water-land interface. Littoral zone organic matter degradation contributes to increasing the nutrient pool needed by aquatic macrophytes.

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