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Nutrient dynamics in the deltaic floodplain of the Lower Paraná River

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With 4 figures and 5 tables in the text

Abstract

Nitrogen and phosphorus concentrations were simultaneously measured in the Lower Paraná R., in a floodplain lake in permanent contact with the river, and the surrounding marsh in the deltaic tidal floodplain of the river, where a variable amount of water is daily exchanged between river and floodplain depending on tidal amplitude, wind-action and river discharge. Suspended matter N & P content was assessed in the Lower and Upper Paraná and Bermejo Rivers, together with the lake bottom and marsh sediments. Nitrogen and P exchange in the lake sediment-water interface was estimated by means of cores laboratory incubations. Nutrient limitation for plant growth was studied by means of bioassays. A large suspended matter and nitrate decrease from the river to the lake and marsh was observed. SRP decreased from the river to the lake surface, but increased in the suboxic lake bottom, the water hyacinth ring and the marsh, as well as oxygen depleted cores incubations. Present results suggest that the deltaic floodplains represent a sink of N and a source of SRP, derived from river suspended matter. Differences in N & P concentrations between the Middle and Lower Paraná stretches were consistent with this fact. *Schoenoplectus californicus*, the dominant macrophyte in the marsh was shown to be N limited. Evidence was presented suggesting N limitation for *Eichhornia crassipes*, the dominant macrophyte in the lake. Phytoplankton bioassays did not provide a definite pattern probably shifting frequently from nutrient to light limitation.

Introduction

With an area of $3.1 \cdot 10^6\,km^2$ and a mean discharge of $25{,}000\,m^3\,s^{-1}$ at the mouth, the Paraná R. watershed is the second largest hydrographic system in South America, after that of the Amazon R. The Paraná R. itself, and the Paraguay R., its main affluent (Fig. 1), are fringed for a large part of their courses by a 10–50 km wide floodplain, accounting for an area of $60{,}000\,km^2$ roughly half of it being occupied by a complex network of alluvial levees, meander

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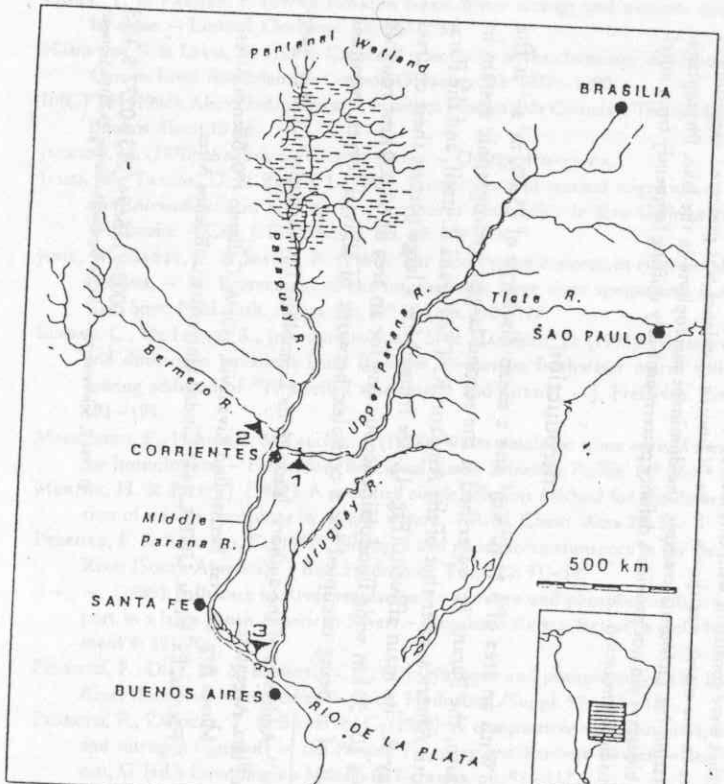

Fig. 1. The Paraná R. basin. Numbers 1 and 2 show sampling points for suspended matter at the Upper Paraná and Bermejo rivers, respectively. Number 3 shows the study site at Zarate, where most of the work took place.

scrolls and ox-bow lakes, the rest being covered by marshes and riparian forests. These waterbodies, colonized by floating macrophytes, mainly water hyacinth (*Eichhornia crassipes*), are generally small (100–500 m wide, 500–3,000 m long), shallow (1–6 m), turbid and productive.

The extended floodplains of these rivers, together with those of the Amazon and Orinoco Rivers represent the most extended lentic habitats in South America. Floodplains lakes are different from most other aquatic habitats in that dramatic changes in water chemistry and biotic communities are attained in response to periodic perturbation by the river flood phase. Both, the Amazon and the Orinoco have been extensively studied; Sioli (1984) summarized most research carried out in the Amazon Basin, and Weibezahn et al. (1990) reviewed most of the present knowledge on the Orinoco Basin. Within the Paraná R., although the main sequences of events have been qualitatively described by Bonetto (1975), detailed information on nutrient status and the processes leading to broad nutrient variations in the floodplain lakes are relatively scarce and limited to the Upper and Middle stretches (Pedrozo et al. 1992, Carignan & Neiff 1992). Nutrient supply from the river, during floods, has been invoked to explain high productivity of floodplain lakes and floodplains in general (Junk et al. 1989). Mass balance of Lake Tineo (Hamilton & Lewis 1987) showed net retention of incoming river carbon, nitrogen and phosphorus in the Orinoco floodplain lakes. Fisher & Parsley (1987) suggested that annual flooding results in significant removal of nitrate and phosphate from the river system in the Amazon basin, a conclusion which was similarly attained by Pedrozo et al. (1992) in the Middle Paraná stretch, at Corrientes, 1,000 km upstream its mouth. Compared with the Amazon and Orinoco Rivers, it seems that water level fluctuations are of less amplitude and shorter duration in the Paraná Basin, and that coverture by water hayacinth is much more important in the latter.

At Rosario, about 300 km upstream from the mouth, the river is divided in two main branches delimiting a vast delta of roughly 15,000 km². Thre present study is aimed to provide an insight on the mayor nutrient sources and pathways, seasonal variations and reciprocal influence between river and floodplain environments within the Lower Paraná Delta, a region which is different from the upper stretches in that it is subjected to tidal influence, water level fluctuations are comparatively dampened and marshes occupy a much larger area than lakes within the plain (roughly 80 % of the total area).

Material and methods

Study site

This study was performed at Zarate (34° 10′ S; 59° 00′ W), in the deltaic floodplain of the Lower Paraná R., about 70 km upstream from the river mouth (Fig. 1). Three different environments were simultaneously sampled: the river, a floodplain lake and the surrounding marsh. The lake has an area of 4.6 ha and is partially covered by a ring of water hyacinth. It is in permanent contact with the river through a short channel of 50 m clogged with macrophytes. Sometimes, when the river stage height changes abruptly, other channels are opened through the ring of macrophytes. Water depth changed with river stage height. Although maximum depth ranged 6–8 m, most of the lakes area was comprised in the 2–3 m range. The lake was sampled in the open water, at surface and bottom, and within the meadows of water hyacinth. The area covered by the water hyacinth ring decreased in winter to roughly ⅓ of the total lake surface and increased in summer to about half of it. The marsh, permanently flooded, was covered by *Schoenoplectus californicus* and *Cyperus giganteus*. At the sampling area, water height variations in the river follows the tidal cycles, a large but variable amount of water is daily exchanged between the river and the floodplain, its magnitude depending on tide amplitude, wind action and river discharge.

The three environments were monthly sampled from November 1990 to February 1992, and again in July 1992, in occasion of the unusually large flood of 1992, the largest in the century.

Water analysis

Water samples were filtered on Whatman GFC and Sartorius membrane filters for nutrient determinations: SRP (molibdate-ascorbic), total phosphorus (acid digestion), nitrates (cadmium column reduction), nitrites (diazotation), and total nitrogen (Kjeldahl) were determined following Strickland & Parsons (1968). Ammonia (indophenol blue) was measured according to Mackereth et al. (1978). Dissolved oxygen (Winkler), calcium and magnesium (EDTA), sodium and potassium (flame photometry), bicarbonate (titrimetric with heliantine), sulfate (turbidimetry) and chloride (titration with silver nitrate) were determined following APHA (1985).

Sediment analysis

Eleven samples of suspended matter were taken in the Lower Paraná R. at Zarate, and analyzed together with 4 samples from the Upper Paraná R. and 5 from the Bermejo R. (Fig. 1), taken in a previous study (Bonetto et al. 1992). Suspended matter from 100 l river water were sedimented in the laboratory; the supernatant discharged by siphon and the sediments dried at 60 °C. Occasionally SRP was determined in the supernatant, and compared to river SRP concentrations; differences were always less than 10 %.

Bottom sediments in the lake and the surrounding marsh were sampled with Plexiglass corers of 4.5 cm of diameter. Total phosphorus (TP) in the sediments was measured by the ignition method (Andersen 1979). P fractionation in both, suspended matter and bottom sediments, was performed following Psenner et al. (1988). Successive extraction were: ammonium chloride (NH_4Cl) 1 M, 2 h; ditionite-bicarbonate (BD) 0.11 M, 1 h; sodium hydroxide (NaOH) 1 M, 18 h; and hydrochloric acid (HCl) 0.5 M, 18 h. After each extraction the samples were centrifuged 10' at 5,000 RPM, and SRP determined in the supernatant. The difference from TP and extracted P is termed nonreactive P (NRP).

Sediment-water exchange

N & P exchange between the sediment-water interface within the lake was studied following Psenner (1984), through laboratory incubations of undisturbed sediment cores together with its overlying lake water. The samples were taken in the border of the water hyacinth ring, representative of most of the lake bottom. The cylinders, 4.5 cm diameter and 45 cm height, were incubated in the dark at room temperature for two weeks. Changes in oxygen, SRP, N-NH_3 & N-(NO_3+NO_2) concentrations in the water during incubation were followed. Methods were slightly modified for operating with small water volumes, so that small aliquots were taken four times during the incubation. Two treatments were assayed; an oxygenated one, achieved by bubbling air at a rate that mixed the supernatant without any visible disturbance of the sediment surface, and an anoxic treatment attained by sealing the surface with liquid Vaseline. Five replicates of each treatment were performed.

Bioassays

Phytoplankton bioassays were performed by laboratory incubation of unmodified river water (controls) together with samples enriched with 10 mg N l^{-1} as KNO_3 and 1 mg P l^{-1} as HK_2PO_4. Incubations were done in 250 ml Erlenmeyer flasks illuminated with fluorescent lamps providing 3200 luxes during 16 hs a day, at room temperature. Phytoplankton density and composition was determined by counting 5 ml subsamples in an Utermohl inverted microscope. Three samples were taken along a 10–15 day incubation period. All bioassay treatments were carried out by triplicate.

Growth rates of *Schoenoplectus californicus* plants were compared in controls against N & P enriched treatments. Nine small plants were transplanted to 45 cm diameter plastic tanks, together with 600 gr dw of homogenized marsh sediments and flooded permanently with distilled water. P replicates received the equivalent to 8 g P m^{-2} as Na_3PO_4 in split applications injected to the sediments twice a month. N replicates were enriched with 20 g N m^{-2} as $(NH_4)_2SO_4$ applied in the same way as P. Growth was attained at ambient temperature, with solar light. Growth was monitored by measuring plant length every week and converting it to biomass with a height-dry weight correlation from 170 individuals harvested in the field. After three months, plants were harvested, total dry weight measured, and N & P plant content determined after Jackson (1970).

A bioassay was performed with *Eichhornia crassipes* (water hyacinth) by transplanting 6 small plants, together with lake water and sediments sampled simultaneously, to 45 cm diameter plastic tanks. Enrichments were done as in *S. californicus* bioassays. Incubation was performed at natural sun light and ambient temperature. Statistical significance of differences between means were assessed through ANOVA analysis (SYSTAT, 3.0 program).

Interstitial water

N & P concentrations in interstitial sediment water in the lake were measured following Carignan et al. (1985), by submerging a device ("peeper") of Plexiglass (30 × 15 × 2 cm) in which 6.5 × 0.6 × 0.6 cm chambers spaced 1 cm center to center were machined, and covered with Gelman DM 450 polisulfure membrane and a 0.2 cm thick Plexiglass sheet with apertures matching the chambers. The membrane and window were fastened to the main body of the dialyzer with stainless screws. The dialyzers were filled with deionized water and inserted into the sediments for one week. Upon retrieval, they were immediately sampled by directly puncturing the membrane with the plastic tip of an automatic pipette. The samples were stored in glass vials preacidified and kept in cold until analyzed a few hours latter.

Results

The river: most physical and chemical recorded variables did not show any seasonal pattern. Mean values are summarized in Table 1. Phosphorus was mainly transported in particulate form, being mean SRP concentration (24 $\mu g\, l^{-1}$) 7 % compared to that of TP (338 $\mu g\, l^{-1}$). Suspended matter showed higher values from Feb. 91 to June 91 (270–310 mg l^{-1}), in coincidence with the flood of the Bermejo R. (Fig. 1), and lower ones for the rest of the year (20–50 mg l^{-1}). Mean total P content and P fractionation in the suspended matter of the Lower Paraná R., together with those of the Upper Paraná and

Table 1. Mean concentration and standard deviation of measured chemical parameters in the Lower Paraná R., a floodplain lake, and the surrounding marsh, (* not measured).

	River	Lake			Marsh
		Open water		Water	
		Surface	Bottom	Hyacinth	
Cond. ($\mu S\ cm^{-1}$)	129 ± 22	137 ± 22	137 ± 24	141 ± 21	125 ± 25
pH	7.4 ± 0.4	6.9 ± 0.3	6.8 ± 0.3	6.4 ± 0.4	6.3 ± 0.5
Oxygen $mg\ l^{-1}$	6.9 ± 1.5	4.2 ± 0.9	2.0 ± 2.2	1.3 ± 1.0	2.0 ± 1.2
Susp. Matter $mg\ l^{-1}$	120 ± 116	29 ± 58	16 ± 16	105 ± 57	11 ± 15
TP ($\mu g\ l^{-1}$)	338 ± 242	207 ± 117	285 ± 120	360 ± 55	*
SRP ($\mu g\ l^{-1}$)	24 ± 15	18 ± 23	76 ± 74	72 ± 67	76 ± 97
N ($NO_3^- + NO_2^-$) ($\mu g\ l^{-1}$)	195 ± 132	31 ± 35	30 ± 32	81 ± 176	15 ± 18
NNH_4^+ ($\mu g\ l^{-1}$)	55 ± 58	57 ± 33	150 ± 203	125 ± 199	42 ± 54
IN ($\mu g\ l^{-1}$)	250 ± 162	91 ± 34	208 ± 209	225 ± 258	59 ± 43
HCO_3^- ($mg\ l^{-1}$)	46 ± 08	50 ± 05	59 ± 17	57 ± 13	*
Na^+ ($mg\ l^{-1}$)	16 ± 07	17 ± 05	15 ± 06	11 ± 02	*
K^+ ($mg\ l^{-1}$)	3 ± 0.3	3 ± 1.0	4 ± 1.0	5 ± 1.5	*
Cl^- ($mg\ l^{-1}$)	15 ± 4	15 ± 4	13 ± 5	13 ± 3	*
Ca^{++} ($mg\ l^{-1}$)	9 ± 3	10 ± 2	12 ± 3	13 ± 4.	*
$SO_4^=$ ($mg\ l^{-1}$)	29 ± 14	17 ± 6	21 ± 7	21 ± 12	*

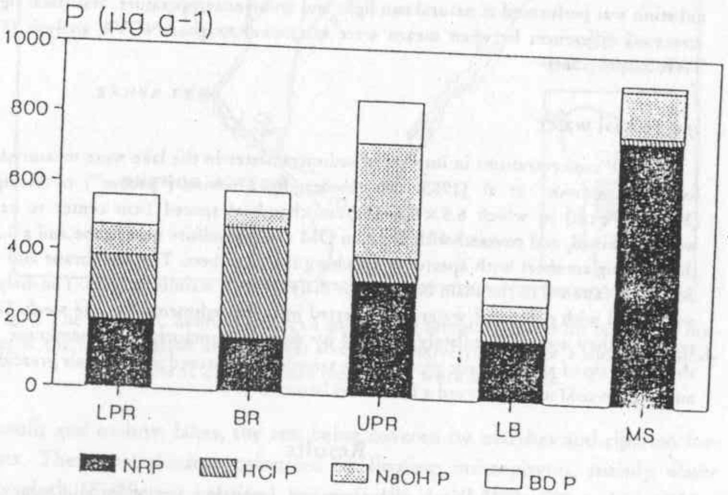

Fig. 2. Total P, and P fractionation of suspended matter from the Lower Paraná (LPR), Bermejo (BR), and Upper Paraná (UPR) rivers, together with lake bottom (LB), and marsh soil (MS) samples.

Bermejo Rivers, its two main contributors, are shown in Fig. 2. The samples from Upper Paraná and Bermejo Rivers were quite different: those of the former had higher TP content, being the NaOH and NRP extractable P the main fractions, while those of the latter had lower TP content, being the HCl extractable P the main fraction. The samples from the Lower Paraná R. resembled those of the Upper Paraná R., in Nov. 90 and Jan. 91, and resembled those of the Bermejo R. the rest of the year. Inorganic N represented roughly half of the TN pool ($510\ \mu g\ l^{-1}$), being nitrate the main component ($194\ \mu g\ N\ l^{-1}$), followed by ammonia ($55\ \mu g\ N\ l^{-1}$) being nitrite always below $4\ \mu g\ N\ l^{-1}$. The mean TN content of the suspended matter was 0.14% (Fig. 3), intermediate between those of the Upper Paraná and the Bermejo Rivers, showing little variations through the sampling period. Mean IN/SRP ratio, by weight, was 11 while mean TN/TP resulted 2.2.

Water transparency was low throughout the year with Secchi depth ranging from 9 to 36 cm. Phytoplankton density was low in most of the sampling dates ($90-500\ ind.\ ml^{-1}$), with the exception of Oct.–Nov. 91 ($1600-3100\ ind.\ ml^{-1}$), in coincidence with the lowest water stage height recorded. Phytoplankton composition showed the absolute dominance of diatoms (60–90% of total cell density), and, within them, of *Aulacoseira granulata* var. *granulata* and var. *angustisima* (32–84% of total cell number), sometimes followed by *Lyngbya limnetica*, *Actinocyclus* sp. and *Aphanocapsa* sp., always in low numbers. From the three bioassays carried out with water from the Lower Paraná R. (Fig. 4), in two of them (Nov. 90, and Nov. 91), nutrient addition did not yield significant increases of cell numbers over the control, while the one performed on May 91 showed maximum phytoplankton development in the treatment enriched with N.

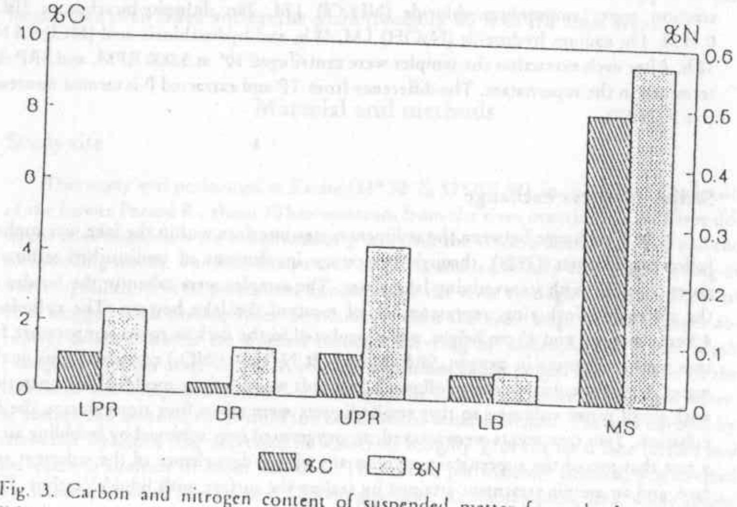

Fig. 3. Carbon and nitrogen content of suspended matter from the Lower Paraná (LPR), Bermejo (BR) and Upper Paraná (UPR) rivers, together with lake bottom (LB) and marsh soil (MS) samples.

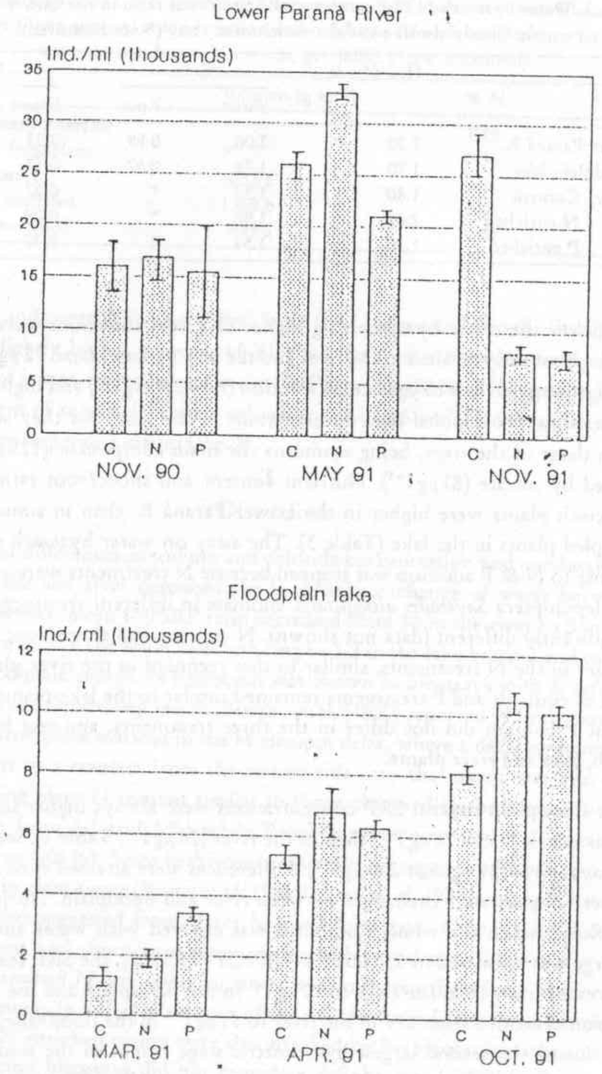

Fig. 4. Maximum phytoplankton density (ind. ml^{-1}) attained in controls and in N & P enriched incubations in the Lower Paraná River and a floodplain lake. Bars show standard deviation.

The lake: Sodium and chloride concentrations, and conductivity throughout the year were correlated with those of the river water (0.77, 0.85, 0.79 respectively, $p < 0.05$), without any significant difference in mean concentration between them (Table 1). Suspended matter was, nevertheless, 24 % compared to that of the river, while transparency was three times larger (Secchi lecture ranged 20–110 cm). Water pH decreased from the river to the lake surface to the lake bottom, being lowest in the water hyacinth ring (Table 1), in a trend opposite to that of Ca concentration which increased in the same sequence. Sulfate within the lake was 62 % compared to that in the river. The lake stratified from October to March: temperature differences from surface to bottom increased until late summer attaining 8 °C in Feb. Dissolved oxygen, at surface, was low throughout the year ranging from 2.6 to 5.3 mg l^{-1}, becoming undetectable at the bottom during stratification.

Mean TP and SRP were lower in the lake surface than in the river (61 and 75 %, respectively) (Table 1). At surface SRP concentrations were lower during the stratification period; becoming undetectable in the summer of 1991 (Jan.–Feb.) and attaining 7 μg l^{-1} in Feb. 92. On Aug. and Oct. 91, the lake became dark colored after intense precipitations, suggesting washing off humic-like compounds from the surrounding macrophytes and terrestrial vegetation. In this case SRP was unusually high (44–76 μg l^{-1}), higher than in the river. Towards the bottom SRP and Ca concentrations were higher than on surface throughout the year. SRP increased progressively during stratification period attaining 250 μg l^{-1} in late summer (Feb. 92).

Table 2 shows the exchange of SRP in the water sediment interface of laboratory incubated sediment corers. The oxygenated treatments succeeded in producing supersaturation, while the anoxic treatments did not attain complete anoxia in the water column. Dissolved oxygen was below 1 mg O_2 l^{-1} and a black sedimentary surface was observed in the superficial sediments. Disappearance of SRP from water when air was bubbled, gave quite similar patterns (2.4–3 mg P m^{-2} d^{-1}) in the incubations from Aug. to Nov., and lower in late summer (Feb. 92, 0.4 mg P m^{-2}). However, when oxygen was depleted, release of 3–25 mg P m^{-2} d^{-1} from the sediments was recorded. Concentrations of SRP in the interstitial water of bottom lake sediments showed an increase from 1.02 mg P l^{-1} at the superficial sediments up to 1.45 mg l^{-1} at 12 cm depth, decreasing downwards. Superficial bottom lake sediments showed almost half

Table 2. Net flux of SRP & IN (mg m^{-2} d^{-1}) and final IN/SRP ratio in incubations of undisturbed cores from lake bottom. (– indicates fluxes from the water to the sediments; * not measured).

Assay	Mean water	Oxygenated			Oxygen Depleted		
	temp. (°C)	SRP	IN	IN/SRP	SRP	IN	IN/SRP
Aug. 91	14	–2.4	*	3	25	–4	0.5
Oct. 91	18	–3	–8	3	3	–5	0.5
Nov. 91	24	–3	12	0.4	17	15	0.3
Feb. 92	29	–0.4	20	7	8	28	1

TP content compared to the suspended matter from the river (Fig. 3), being NRP the main fraction: 48 %, against 34 % in the river, while the HCl extractable fraction decreased from 33 % in the river to 18 % in the lake.

Nitrates were strongly reduced from the river (mean 194 $\mu g\, l^{-1}$) to the lake (mean 31 $\mu g\, l^{-1}$) while ammonia was similar (55 against 57, respectively). At the surface lower IN concentrations were found during the stratification period, (7 $\mu g\, l^{-1}$, in Jan. 91). When the water became dark colored, high ammonia (90–160 $\mu g\, l^{-1}$) together with low nitrate concentrations (7–8 $\mu g\, l^{-1}$) were recorded. At the bottom, nitrates became depleted during stratification periods becoming undetectable in late summer, while ammonia showed the opposite trend increasing up to 560 $\mu g\, N\, l^{-1}$ in Feb. 92. Mean Kjeldahl N was not significantly different in the river and the lake (510 against 516 $\mu g\, l^{-1}$, respectively). The exchange of IN in the sediment-water interface of incubated cores was shown to be strongly dependant upon incubation temperature (Table 2). At higher temperatures prevailing in Nov. 91 and Feb. 92 (mean of 24 and 29 °C, respectively) IN accumulated in the overlying water, irrespective of its oxygen content; while at lower ones prevailing in Aug. and Oct. 1992 (mean 14 and 18 °C, respectively) IN disappeared from the overlying water irrespective of its oxygen content. IN/SRP ratios at the end of the incubations ranged from to 0.4 to 7 in the oxygenated incubations and from 0.3 to 1 in the oxygen depleted ones. In the interstitial water of bottom sediments sampled on Nov. 91 nitrates were undetectable and ammonia concentration increased from 3.15 $mg\, N\, l^{-1}$ at the sediment surface, up to 4.53 $mg\, N\, l^{-1}$ at 12 cm depth, and decreased downwards. IN/SRP in the interstitial water was roughly 3 at all depths. Total N content of bottom lake sediments was lower than of river suspended matter content (0.05 and 0.14 %, respectively, Fig. 3).

Phytoplankton density was low in most of the sampling dates (140–600 ind. ml^{-1}), attaining higher densities in a few cases in Fall (March 91: 1,700 ind. ml^{-1}) and spring (Oct.–Nov. 91: 2,000 and 1,060 ind. ml^{-1}, respectively). Phytoplankton composition was different to that in the river being Cryptophyceae (represented mainly by *Cryptomonas* sp.) and Euglenophyceae (represented mainly by *Euglena* spp., *Trachelomonas* spp. and *Mallomonas* spp.) the dominant groups. *Cryptomonas* sp. ranged 30–84 % of total cell number in all sampling dates except in Feb. 92, when it represented 13 % and Euglenophyceae represented 44 % of the total. Cryptomonas dominance was especially evident during the dark colored water periods when attaining 74 and 84 % of the total cell numbers in Aug. and Oct. 91, respectively. Diatoms, dominant in the river, represented 1–22 % of total cell number, with higher percentages in coincidence with dates of larger water exchange. Enrichment bioassays showed increased densities in the P enriched treatments on March 91, no significant differences on April, while in Oct. both N & P enrichment showed increased densities with respect to the control, without differences between them (Fig. 4).

Table 3. Water hyacinth N & P content and shoot/root ratio in the Lower Paraná R., the floodplain lake and the enrichment assay (* not measured).

	Shoot/root	% N		% P	
		Shoot	Root	Shoot	Root
Lower Paraná R.	2.30	2.06	0.89	0.23	0.17
Floodplain lake	1.70	1.74	0.57	0.17	0.14
Assay: Control	1.80	1.53	*	0.27	*
N enriched	2.01	1.96	*	0.28	*
P enriched	1.30	1.54	*	0.30	*

Below the water hyacinth ring higher SRP concentrations were recorded throughout the year than in the river and the lake surface (mean 72 $\mu g\, l^{-1}$, Table 1) together with low oxygen concentration (nd–2.4 $mg\, l^{-1}$) and higher Ca concentrations. IN doubled the concentrations in the lake, but they were lower than those of the river, being ammonia the main component (125 $\mu g\, l^{-1}$), followed by nitrate (81 $\mu g\, l^{-1}$). Nutrient content and shoot/root ratio in water hyacinth plants were higher in the Lower Paraná R. than in simultaneously sampled plants in the lake (Table 3). The assay on water hyacinth growth response to N & P addition was stopped because N treatments were attacked by the lepidoptera *Sameodes albiguttalis*. Biomass in different treatments was not significantly different (data not shown). N content and shoot/root ratio were higher in the N treatments, similar to that recorded in the river plants, while that of controls and P treatments remained similar to the lake plants (Table 3). Plant P content did not differ in the three treatments, and was higher than both, lake and river plants.

The floodplain marsh: SRP concentrations were always higher in the floodplain marsh (mean 76 $\mu g\, l^{-1}$) than in the river (24 $\mu g\, l^{-1}$, Table 1), while IN was always lower (59 against 250 $\mu g\, l^{-1}$). Differences were attained even when large water volumes were exchanged between river and floodplain. During the July 92 flood, when the whole floodplain was covered with water and river discharge was estimated in 33,000 $m^3\, s^{-1}$ (INCYTH 1992), the SRP concentration increased from 16 in the river to 22 $\mu g\, l^{-1}$ in the floodplain and the IN concentration decreased from 279 in the river to 11 $\mu g\, l^{-1}$ in the floodvalley. On Nov. 90, during the second largest hydrometric stage height of the studied period, SRP concentration increased from 17 in the river to 31 $\mu g\, l^{-1}$ in the floodplain, and IN decreased from 91 $\mu g\, l^{-1}$ in the river to below detection in the floodplain. N & P content in *Schoenoplectus californicus* plants simultaneously sampled in the river side roughly doubled that of plants sampled 2 km inside the floodplain (Table 4). Bioassays showed higher growth rates in *Schoenoplectus californicus* enriched with N, while P enrichment and controls did not differ. Both, N & P content was higher in plants enriched with N, while P en-

Table 4. Biomass and N & P content of *Schoenoplectus californicus* in the enrichment assay and in plants sampled at the riverside, and inside the floodplain. The same letter denote not significant differences, ($p < 0.05$). (* not measured).

	Biomass (g m^{-2})	% N	% P
Lower Paraná riverside	*	1.15	0.27
Inside the floodplain	*	0.56	0.13
Assay: Control	1033 a	0.94	0.21
N enriched	1365 b	1.61	0.26
P enriched	999 a	1.03	0.21

richment and controls did not differ. Superficial sediments from the floodplain showed slightly higher amounts of TP than the river suspended matter (Fig. 2); most of it was, nevertheless, in the NRP fraction (82 %). Nitrogen and carbon content of superficial marsh sediments resulted 5 and 7 times higher than in the river suspended matter (Fig. 3).

Discussion

Lack of differences in sodium and chloride concentration and conductivity between lake and river described the large daily exchange of water between them. However, mean IN/SRP ratio decreased from 10 in the river to 5 in the lake surface to 3 in the water hyacinth ring to 1.2 in the lake bottom and to 0.8 in the flood-plain marsh. N limitation was shown in bioassays with *S. californicus* from the floodvalley marsh. Buresh et al. (1980) reported N limitation in *Spartina alterniflora* marshes in the Mississippi delta, where a decrease in nutrient content in a transect from the stream side into the marsh was also observed, being plant N content similar to those observed in the present study (decreasing from 1.1 to 0.6 %) while P content was quite lower (decreasing from 0.15 to 0.04 %). Since herbivores respond to changes in relative amount of protein in plant tissue (Vince et al. 1981, Curtis et al. 1989), nitrogen limitation was also suggested from water hyacinth bioassays. Changes in N & P plant content and shoot/root ratio reinforce this evidence. Carignan et al. (1992) determined N limitation for water hyacinth growth in large limnocorrals experiments in a floodplain lake of the Middle Paraná stretch, at Corrientes, where N enriched plants were also attacked by herbivores (grasshoppers). Phytoplankton bioassays did not provide a definite trend. Within the river, light limitation was suggested by lack of response to nutrient addition, low phytoplankton densities and high turbidity and nutrient content of river water. Light limitation was shown to occur in the Upper and Middle Paraná stretches, where diatoms were also the dominant group (Bonetto et al. 1983). Reynolds (1984) suggested that higher photosynthetic efficiency, higher chlorophyll content and lower threshold for light saturation confer diatoms a competitive advantage in turbid, well mixed environments. Within the lake, phytoplankton composition was the same as reported for floodplain lakes in the Middle Paraná stretch (Pedrozo et al. 1992). Motile forms of Cryptophyceae and Euglenophyceae have an adaptative advantage in an environment in which light and nutrient resources are vertically segregated. Bioassays suggested that both nutrients were limiting during pulses of high phytoplankton density. It seems likely that nutrient and light limitation shifts frequently depending on external conditions such as wind erosion of the stratification gradient, the daily amount of water exchanged with the river, rain derived inputs from the surrounding marsh, daily irradiance, etc. Carignan & Planas (1992) reported that several floodplain lakes were N limited while others were light limited, in the Middle Paraná stretch, at Corrientes, and pointed out that different approaches such as bottle incubation, limnocorrals, whole lake fertilization, yielded different results. Factors other than light and nutrient may also influence phytoplankton development within the lake. Several species of both, Cryptophyceae and Euglenophyceae, dominating the lake phytoplankton were shown to be phagotrophic (Porter 1988). Burkholder (1992) mimicked the effect of river suspended load on lake phytoplankton by studying the effect of clay inputs on phytoplankton behavior and P uptake. Clay addition increased phytoplankton uptake of added ^{32}P-phosphate. Aggregates of cells and particles were formed, extracellular cytoplasmic webs of netlike extensions and pedyncles were interpreted as indicatives of phagotrophic and saprotrophic nutrition. Serrano & Guisande (1990) showed that tanine inputs from the surrounding vegetation influenced phytoplankton density and composition in small peridiune deltaic ponds of the Doniana National Park, Spain. Primary production in the lake is mainly restricted to macrophyte growth; within the water column, bacterial food webs remain to be assessed but it seems feasible that they represent a rather important pathway.

The suspended matter input from the river was either trapped by the macrophyte root system or deposited on the lake bottom. The lower TP content and HCl extractable P fraction in superficial bottom sediments together with higher SRP and Ca concentrations in the lake water towards the bottom and below the water hyacinth ring, throughout the year, suggest a release of Ca bound P from the incoming river suspended matter. Cores incubations showed further release of SRP in response to oxygen depletion in agreement with accumulation of SRP towards the bottom during summer stratification. The lower recorded flux (3 mg m^{-2} d^{-1}) was probably due to insufficient oxygen depletion in that treatment, being higher rates recorded when depletion was improved (8 – 25 mg m^{-2} d^{-1}). Thus, the Bd extractable P fraction of the river suspended matter was later released within the lake and was partially available for plant growth. Our estimated release rates lie towards the upper literature quoted range: 15 – 18 mg P m^{-2} d^{-1} in eutrophic Eau Gaule reservoir

(James et al. 1992), 40 mg P $m^{-2} d^{-1}$ in hypertrophic lake Sobygaard (Sondergaard 1991) and were similar to the 12–21 mg P $m^{-2} d^{-1}$ reported by Carignan & Neiff (1992) for floodplain lakes in the Middle Paraná stretch, at Corrientes.

Bottom lake sediments contained less N than incoming river suspended matter, a result consistent with high IN release rates assessed in cores incubations during the period of higher temperatures (Table 2) and observed ammonia accumulation towards the bottom during the stratification period. Results from the sediment water incubations showed the overwhelming influence of temperature. Denitrification, together with bacterial uptake caused IN disappearances in the incubations at lower temperatures. As complete deoxygenation was not attained, it seems likely that the ammonia released from the bottom was nitrified in the water column and later denitrified in water sediment interface, in the oxygen depleted treatments. Within the incubations with oxygenation at higher temperatures, mineralization of organic matter strongly enhanced ammonia release from sediments to account for the IN accumulation in spite of the ongoing losses. Measured IN release rates from the bottom at higher temperatures were similar to the 7–24 mg $m^{-2} d^{-1}$ reported by Carignan & Neiff (1992), at Corrientes. Large differences in nitrate concentration between the river and the lake in spite of large volumes of water daily exchanged suggests a large net input of nitrogen from the river. Since not important accumulation was observed in the bottom, present evidence suggests that denitrification accounts for a large portion of the incoming N. Carignan & Neiff (1992) claimed that denitrification rates were below their detection limit in a floodplain lake in which nitrates were undetectable during most of the studied period. Nevertheless, a great denitrification potential was observed, since added nitrate disappeared in hours. The floodplain lake in which they worked was isolated from the river, receiving river water only after the water stage height became considerably high, occurring one or twice a year. In our lake, where nitrate-rich river water is daily pumped into a suboxic environment, high denitrification rates are expectable. Downes (1988) reported that at low oxygen concentration nitrite formed from ammonia is transformed into molecular nitrogen in a so-called "nitrifying denitrification".

Within the surrounding marsh, nitrate became depleted as river water came into the floodplain suggesting a large net input from the river. Since N content in the marsh sediments is 4 times higher than the river suspended matter content, fixation by macrophytes followed by organic accumulation in the sediment seems an important pathway. Low oxygen concentration in the water and high organic matter content in the sediments suggest that IN losses by denitrification are also plausible. Freshwater marshes have the potential to remove large inputs of IN through denitrification (Lindau et al. 1991). Inputs of ammonia may also be lost by coupled nitrification-denitrification. Reddy et al. (1989) showed that oxygen transport through the air spaces (aerenchyma tis-

Table 5. Mean IN and P concentrations in the Upper Paraná, Paraguay and Bermejo Rivers (Pedrozo & Bonetto 1989, Pedrozo & Bonetto 1987, Pedrozo et al. 1988, respectively), its weighted mean, corrected for discharge differences, and the Lower Paraná River (units are $\mu g\, l^{-1}$).

	Upper Paraná	Paraguay	Bermejo	Weighted Mean	Lower Paraná
$N-NO_3^- + NO_2^-$	257	109	263	233	195
$N-NH_4^+$	89	122	103	95	55
IN	346	231	366	328	250
SRP	10	45	65	19	25
TP	40	120	1300	104	139

sue) of aquatic macrophytes into the root zone supports nitrification of ammonia, with the nitrate diffusing into the adjacent anaerobic zone where it undergoes denitrification. Losses of added ammonia of 102–122 mg N $m^{-2} d^{-1}$ by coupled nitrification-denitrification in different macrophytes were measured by them. Valiela & Teal (1979) reported denitrification rates of 40 mg N $m^{-2} d^{-1}$ at Sippewissett salt marsh, where denitrification doubled N fixation.

At the deltaic floodplains of the Lower Paraná stretch, marshes cover roughly 80% of the floodplain, being riparian forest and lakes about 10% each. Although a net SRP input from the river to the lake was suggested, the high SRP concentrations in the floodplain marshes suggest that, on the whole, a net exportation of SRP from the floodplain together with large nitrate losses were attained (Table 1). If this is so, nutrient concentration along the river should show the corresponding changes along its course. Table 5 shows the mean concentration of inorganic nitrogen and phosphorus in the Upper Paraná, Paraguay, and Bermejo Rivers, which join together at Corrientes, to form the Middle Paraná stretch. The weighted mean, corrected for discharge differences, of the three rivers is calculated and compared with that of the Lower Paraná River, at Zarate, roughly 1000 km downstream. No important affluents are received in by the Middle and Lower Paraná stretches. A decrease in IN concentration (both nitrates and ammonia) and an increase in both SRP & TP is evident. Important cities without sewage treatment plants, industrial settlements and intensive agriculture produce N & P inputs to the Lower Paraná stretch. Thus, increase in SRP & TP is partially due to cultural impact. On the contrary, the observed decrease in IN concentration accounts also for the large human N inputs, and was consequence of river-floodplain interactions.

The sediments of the Lower Paraná River were similar to those of the Bermejo River most of the year. Only during unusually high discharge records of the Upper Paraná River were sediments from the Lower Paraná similar to those. The seston contribution of the Upper Paraná and Bermejo Rivers were estimated as 10^7 and 10^8 ton y^{-1}, respectively (PEDROZO et al. 1988). The Paraguay R. does not provide an important sediment load because it drains the huge Pantanal wetland, (Fig. 1) where lack of relief and extensive plant coverture determines extremely low erosion rates (PEDROZO et al. 1988). The average TP content of the suspended matter from the Lower Paraná River (598 $\mu g\,g^{-1}$) was slightly lower than the weighted mean of that from the Bermejo plus Upper Paraná Rivers (665 $\mu g\,g^{-1}$). Nevertheless, the mean NRP fraction, assumed to be mainly refractory organic P (PSENNER et al. 1988), was higher in the Lower Paraná River (201 $\mu g\,g^{-1}$) than the weighted mean of the Bermejo and Upper Paraná Rivers (175 $\mu g\,g^{-1}$). Mean C content of the seston from the Lower Paraná River (1.07 % dw) was higher than the weighted mean from the Bermejo and Upper Paraná Rivers (0.43 % dw) and so was the N content: 0.14 % against 0.096 % of the later. The C/N ratio increased from 3.75 in the Bermejo River, to 4.81 in the Upper Paraná River, to 7.64 in the Lower Paraná River, suggesting the contribution of organic matter of high C/N ratio from macrophytes and terrestrial vegetation of the floodplain. In the two samples in which the suspended matter from the Lower Paraná R. resembled that of the Upper Paraná R., (Nov. 90 and Jan. 91), the BD extractable P fraction was higher in the former, while in the 8 samples in which the suspended matter from the Lower Paraná River resembled that of the Bermejo River, the NH_4Cl extractable P fraction was higher in the former, suggesting the P contribution from sewage, intensive agriculture and industrial settlements.

Summary

Sodium, chlorine and conductivity were essentially the same in the river and the lake, expressive of the large volumes of water daily exchanged between them (Table 1). Suspended matter was strongly decreased from the river to the lake. SRP decreased from the river to the lake surface but increased in lake bottom, the water hyacinth ring and the surrounding marsh (Table 1). Lake bottom sediments showed lower TP content than the river suspended matter, and a lower HCl extractable P fraction (Fig. 2), suggesting, together with the higher Ca concentration and lower pH values in the lake water, that the calcium bound P of the incoming river suspended matter is partially released within the lake. High SRP concentrations during suboxic conditions attained in the lake bottom at the stratification period, in the marsh throughout the year, and observed in cores laboratory incubations (Table 2) suggest that the iron bound P of the incoming river suspended matter is also released within the floodplain environment. The large decrease of nitrates from the river to the lake and the surrounding marsh (Table 1) suggests a large net input of nitrogen from the river to the floodplain environment, decreasing the IN/SRP ratio from 10 in the river, to 5 in the lake surface, to 2.8 in the water hyacinth ring to 2.4 in the lake bottom to 0.75 in the marsh. Bottom lake sediments had lower TN content than the incoming river suspended matter (Fig. 3), consistent with the high ammonia concentration prevailing towards the bottom during stratification and observed high release rates from the sediments in the cores incubations at higher temperatures (Table 2). Therefore, present evidence suggest that the deltaic floodplain of the Lower Paraná R. represent a sink of N and particulate P, and a source of SRP, derived from river suspended matter. Comparison of estimated IN & SRP concentrations in the Middle Paraná with those of the Lower Paraná stretch (Table 5), is consistent with this pattern. *Schoenoplectus californicus*, (Table 4) the dominant macrophyte in the marsh, was shown to be N limited. Evidence was presented that *Eichhornia crassipes* (water hyacinth) was also N limited (Table 3). Phytoplankton, nevertheless, did not provide a conclusive pattern (Fig. 4). Diatoms, the dominant in the river, were light limited while Cryptophyceae, the dominant in the lake, probably shifted frequently from nutrient to light limitation, being both nutrients limiting pulses of high densities. These patterns are similar to those described previously for floodplain lakes in the Middle Paraná stretch, at Corrientes, 1000 km upstream (PEDROZO et al. 1992), and represent widespread features of the large floodplain systems of the Paraná R.

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References

ANDERSEN, J. (1979): An ignition method for determination of total phosphorus in lake sediments. – Water Res. 10: 329–331.

APHA (1985): Standard Methods for the examination of waters and wastewaters. – American Public Health Assoc. N.Y., 874 pp.

BONETTO, A. (1975): Hydrologic regime of the Paraná River and its influence on ecosystem. – In: HASLER, A. (ed.): Coupling of land and water systems. – Springer, Berlin, New York, pp. 175–197.

BONETTO, C., GABELLONE, N. & POIRE, D. (1992): Phosphorus fractionation of suspended matter from the Paraná and Bermejo rivers. – Verh. Int. Verein. Limnol. (subm.)

BONETTO, C., ZALOCAR, Y. & VALLEJOS, R. (1983): Fitoplancton y producción primaria del río Alto Paraná. – Physis. 41 (101): 81–93.

BURESH, R., DELAUNE, R. & PATRICK, W. (1980): Nitrogen and phosphorus distribution and utilization by *Spartina alterniflora* in a Louisiana Gulf coast marsh. – Estuaries 3: 111–121.

BURKHOLDER, J. (1992): Phytoplankton and episodic suspended sediment loading: Phosphate partitioning and mechanisms for survival. – Limnol. Oceanogr. 37: 974–988.

CARIGNAN, R. & NEIFF, J. (1992): Nutrient dynamics in floodplain ponds of the Paraná River (Argentina). – Biogeochemistry (in press).

CARIGNAN, R., NEIFF, J. & PLANAS, D. (1992): Limitation of floating macrophytes by nitrogen in floodplain lakes of the Paraná. – Limnol. Oceanogr. (subm.)

CARIGNAN, R. & PLANAS, D. (1992): Recognition of nutrient and light limitation in turbid mixed layers: three approaches compared in the Paraná floodplain (Argentina). – Limnol. Oceanogr. (subm.)

CARIGNAN, R., RAPIN, F. & TESSIER, A. (1985): Sediment porewater sampling for metal analysis: a comparison of techniques. – Geochim. Cosmochim. 49: 2493–97.

CURTIS, P., DRAKE, B. & WHIGHAM, D. (1989): Nitrogen and carbon dynamics in C_3 and C_4 estuarine marsh plants grown under elevated CO_2 in situ. – Oecologia 78: 297–301.

DOWNES, M. (1988): Aquatic nitrogen transformations at low oxygen concentrations. – Appl. Environ. Microbiol. 54: 172–175.

Fisher, T. & Parsley, P. (1979): Amazon lakes: Water storage and nutrient stripping by algae. – Limnol. Oceanogr. 24: 547–553.

Hamilton, S. & Lewis, W. (1987): Causes of seasonality in the chemistry of a lake on the Ornico River floodplain. – Limnol. Oceanogr. 32: 1277–1290.

INCYTH (1992): Alerta hidrológica. – Instituto Nacional de Ciencia y Técnica Hídrica. Buenos Aires, 10 pp.

Jackson, M. (1970): Análisis químico de suelos. – Omega, Barcelona.

James, W., Taylor, D. & Barko, I. (1992): Production and vertical migration of *Ceratium hirundinella* in relation to phosphorus availability in Eau Galle reservoir, Wisconsin. – Can. J. Fish. Aquat. Sci. 49: 694–700.

Junk, W., Bailey, P. & Sparks, R. (1989): The flood pulse concept in river-floodplain systems. – In: Proceedings of the international large river symposium (LARS), Can. Spec. Publ. Fish. Aquat. Sci. N° 106, pp. 110–127.

Lindau, C., De Laune, R., Jiraponcharoen, S. & Manajuti, D. (1991): Nitrous oxide and dinitrogen emissions from *Panicum hemitomon* freshwater marsh soils following addition of ^{15}N labelled ammonium and nitrate. – J. Freshwat. Ecol. 6: 191–198.

Mackereth, F., Heron, J. & Talling, J. (1978): Water Analysis: some revised methods for limnologists. – Freshwater Biological Assoc. Scientific Public. N° 36.

Murphy, H. & Riley, J. (1962): A modified single solution method for the determination of soluble phosphate in natural waters. – Anal. Chem. Acta 27: 31.

Pedrozo, F. & Bonetto, C. (1987): Nitrogen and phosphorus transport in the Bermejo River (South America). – Rev. Hydrobiol. Trop. 20: 91–99.

– – (1989): Influence of River regulation on nitrogen and phosphorus mass transport in a large South American River. – Regulated Rivers: Research and Management 4: 59–70.

Pedrozo, F., Diaz, M. & Bonetto, C. (1992): Nitrogen and phosphorus in the Paraná River floodplain waterbodies. – Arch. Hydrobiol./Suppl. 90: 171–185.

Pedrozo, F., Zalocar, Y. & Bonetto, C. (1988): A comparative study on phosphorus and nitrogen transport in the Paraná, Paraguay and Bermejo Rivers. – In: Tundisi, G. (ed.): Limnología a Manejo de Represas, pp. 91–117.

Porter, K. (1988): Phagotrophic phytoflagellates in microbial food webs. – Hydrobiol. 159: 89–97.

Psenner, R., Bostrom, B., Dinka, M., Pettersson, K., Pucsko, R. & Sager, M. (1988): Fractionation of phosphorus in suspended matter and sediment. – Arch. Hydrobiol. Beih. 30: 98–103.

– (1984): Phosphorus release patterns from sediments of a meromictic meaotrophic lake (Piburger See, Austria). – Verh. Int. Verein. Limnol. 22: 219–228.

Reddy, K., Patrick, W. & Lindau, C. (1989): Nitrification-denitrification at the plant root-sediment interface in wetlands. – Limnol. Oceanogr. 34: 1004–1013.

Reynolds, C. (1984): The Ecology of freshwater phytoplankton. – Cambridge Univ. Press., Cambridge.

Serrano, L. & Guisande, C. (1990): Effects of polyphenolic compounds on phytoplankton. – Verh. Int. Verein. Limnol. 24: 282–288.

Sioli, H. (1984): The Amazon. Limnology and landscape ecology of a mighty tropical river and its basin. – Junk, The Hague.

Sondergaard, M. (1990): Pore water dynamics in the sediment of a shallow and hypertrophic lake. – Hydrobiologia 192: 247–258.

Strickland, J. & Parsons, T. (1968): A practical Handbook for seawater analysis. – Bulletin 167. J. Fish. Res. Bd. Can., Ottawa, Canada.

Valiela, I. & Teal, J. (1979): The nitrogen budget of a salt marsh ecosystem. – Nature 280: 652–656.

Vince, S., Valiela, I. & Teal, J. (1981): An experimental study of the structure of herbivorous insect communities in a salt marsh. – Ecology 62: 1662–1678.

Weibezahn, F., Alvarez, H. & Lewis, W. (1990): The Orinoco river as an ecosystem. – Impresos Rubel, Caracas, Venezuela.

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