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Turbidity and dissolved organic matter as significant predictors of spatio-temporal dynamics of phosphorus in a large river-floodplain system

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Abstract

Phosphorus (P) inputs are increasing in river-floodplain systems, but the factors which influence the dynamics of this nutrient are not clear. To assess P dynamics in this kind of river, the main channel of the Middle Paraná River, 3 anabranches, 9 secondary channels, and 20 lakes (7 permanently connected and 13 temporarily connected to the fluvial system) were sampled. Multiple linear regressions were applied to explain spatio-temporal patterns of P through commonly measured limnological variables. Particulate P increased during the sediment peak (evaluated through turbidity). Soluble reactive P (SRP) was positively associated with dissolved organic matter (DOM, mainly the chromophoric fraction), which increased during high waters in the fluvial system but was highly variable in each kind of aquatic environment. In temporarily connected lakes, vegetated zones dominated by emergent macrophytes displayed the highest SRP and chromophoric DOM concentrations. The flood and sediment peak positively affected P load in the river due to the increase in dissolved and particulate fractions, respectively. In addition, particle-bound alkaline phosphatase activity was positively associated with SRP concentration and load. These results suggest that the sediment peak incorporates particulate P in the system while the floodplain is a P source during floods through exportation of the dissolved fraction. Dissolved P could be largely exported associated with DOM, which stimulates phosphatase biosynthesis by decreasing P bioavailability. The effect of aquatic macrophytes on P dynamics seems to be influenced by DOM exudation. According to these considerations, DOM should be taken into account to analyse P dynamics in river-floodplain systems.

KEYWORDS

aquatic macrophytes, chromophoric dissolved organic matter, hydrosedimentological regime, Middle Paraná River system, particle-bound alkaline phosphatase activity, spatio-temporal patterns of phosphorus

1 | INTRODUCTION

Phosphorus (P) is a key element of eutrophication processes in freshwater systems (Vollenweider, 1990). The increase in its bioavailability has negative implications for overall water quality, including increased turbidity and occurrence of anoxic events (Vollenweider, op. cit.).

In river-floodplain systems, temporal dynamics of P is largely affected by the hydrosedimentological regime. During high waters, the increasing exchange of materials among environments increases the deposition of particle-bound P carried by the river in floodplain lakes (Kiedrzyńska, Kiedrzyński, & Zalewski, 2008). Several authors have pointed out that floodplains reduce the downstream transport of P by acting as storage sites for particles (González-Sanchis, Murillo, Cabezas, Vermaat, & Comín, 2015; Kiedrzyńska et al., 2008; Maine, Suñe, & Bonetto, 2004). In contrast, other authors have shown that floodplains are P sources due to the exportation of the dissolved fraction (Almeida et al., 2015; Fisher & Acreman, 2004; Reavis & Haggard, 2016). The spatial dynamics of P also shows variable trends; while some studies have shown an increasing concentration from the main channel (MC) to the floodplain (Roberto, Santana, & Thomaz, 2009; Villar, de Cabo, Vaithiyanathan, & Bonetto, 1999); other studies have shown the opposite (González-Sanchis et al., 2015; Maine et al., 2004).

Factors influencing P dynamics are highly variable in river-floodplain systems (Ward, Tockner, Arscott, & Claret, 2002). The pulses of high and low water discharges and the gradients from the MC to the floodplain control changes in abiotic and biotic variables (Roberto et al., 2009). It has been widely accepted that dissolved oxygen and pH are important control factors of P dynamics (Maine et al., 2004). However, P dynamics can be influenced by other factors, such as dissolved organic matter (DOM) (Shaw, Jones, & Haan, 2000), suspended solids (Müller, Stierli, & Wüest, 2006), and nutrient bioassimilation (Wang, Ren, Wang, Qian, & Hou, 2015). Biological demand for P is high in floodplain lakes due to the high biomass of aquatic macrophytes (Barbieri & Esteves, 1991). When P is in limited supply, alkaline phosphatase synthesized by aquatic organisms catalyses the liberation of orthophosphate (PO_4^{3-}) from organic compounds to make organically-bound P available for assimilation (Rose & Axler, 1998).

River-floodplain systems are subject to increasing P inputs (Beusen, Bouwman, Van Beek, Mogollón, & Middelburg, 2016). However, it is unclear which factors determine spatio-temporal variability of P. Within this framework, this paper aims to assess the dynamics of P concentration and load in a large river-floodplain system and their relationships with other limnological variables. The MC of the Middle Paraná River and floodplain water bodies were sampled during different hydrosedimentological phases. Given that floodplain environments retain high quantities of particle-bound P during high waters (Maine et al., 2004), it was hypothesized that P load in the river decreases in response to increasing water level.

2 | MATERIALS AND METHODS

2.1 | Study area and sampling sites

The basin of the Paraná River (Figure 1a) covers an area of 3.1×10^6 km^2. This fluvial system discharges approximately 470 km^3 of water and 80×10^6 metric tons of suspended sediments into the sea per year (Drago, 2007).

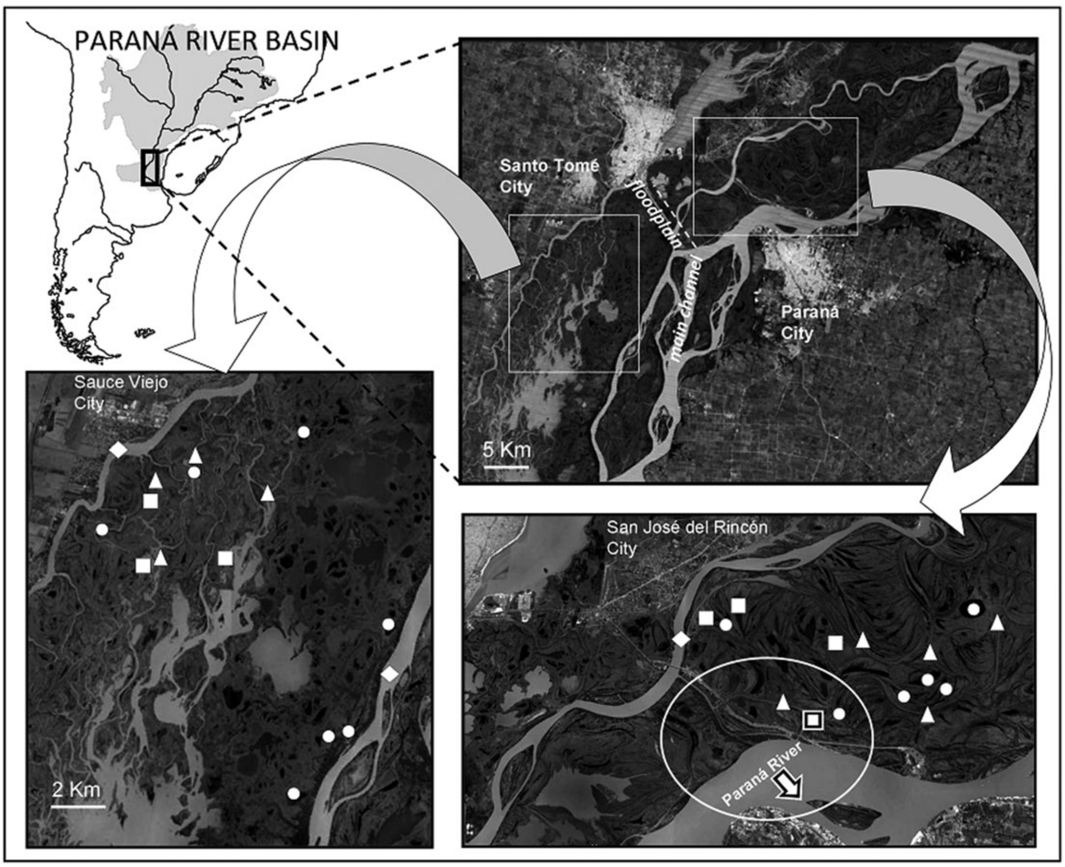

FIGURE 1 Location of the study area. Sampling sites are indicated with an arrow (main channel of the Middle Paraná River), rhombuses (anabranches of the main channel), triangles (secondary channels), squares (lakes permanently connected to the fluvial system), and circles (lakes temporarily connected to the fluvial system). The sites studied in the temporal samplings (2012) are within an ellipse. Sites highlighted with a double border within the ellipse (the main channel and a lake permanently connected to the fluvial system) were sampled both during the temporal samplings and the spatial samplings (2013, 2014, 2015, and 2016). Sites located outside the ellipse were sampled only during the spatial samplings

The Middle Paraná River extends from its confluence with the Paraguay River (27° 29' S; 58° 50' W) to the city of Diamante (Argentina) (32° 4' S; 60° 32' W; Figure 1b). About 50% of the water flows through a well-defined MC. The remaining volume flows through anabranches (AB) divided by islands and bars within the MC. Nearly 75% of the water discharge is from the Upper Paraná River, whereas nearly 90% of the suspended sediments are supplied, through the Paraguay River, via the Bermejo River (Amsler & Drago, 2009). The Middle Paraná River has a 10–50 km wide floodplain (13,000 km^2) along its right bank including lakes permanently connected to the fluvial system (LPC), lakes temporarily connected to the fluvial system (LTC), and secondary channels (SC) forming the floodplain drainage system (Drago, 2007). Cattle production constitutes the preponderant land use activity on the floodplain (Sabattini & Lallana, 2007). Gallery forests grow on the levees, and extensive pastures cover the low areas where *Coleataenia prionitis* (Nees) Soreng is the dominant species. Among aquatic macrophytes, emergent and free-floating species stand out for their biomass and cover surface (Sabattini & Lallana, op. cit.).

The studied sites and periods were selected to represent the spatio-temporal heterogeneity of the Middle Paraná River system. To analyse P temporal dynamics, the MC, SC, LPC, and LTC were sampled approximately fortnightly from February to November 2012 (from here onwards referred to as temporal samplings; Figure 1). This period included two low water phases (one of them coincident with the sediment peak) separated by a flood. Although this sampling design emphasized the analysis of temporal heterogeneity, it also took into account spatial heterogeneity because it included the main kinds of aquatic environments of the system. To analyse P spatial dynamics, four surveys each lasting 10 days (November–December 2013, March–April 2014, September 2015, and February–March 2016) were performed in the MC, three AB, eight SC, seven LPC, and 12 LTC (from here onwards referred to as spatial sampling; Figure 1). The sites sampled to analyse P spatial dynamics not only included the main kinds of aquatic environments of the system but also their different hydrological and morphological features (Devercelli, Scarabotti, Mayora, Schneider, & Giri, 2016). Although this sampling design emphasized the analysis of spatial heterogeneity, it also took into account temporal heterogeneity because it included low (years 2013 and 2014) and high water phases (years 2015 and 2016).

2.2 | Samplings and laboratory analysis

Sample collection was conducted at the centre of the lotic environments and in the pelagic zone of the lakes. At the MC, samples were collected at a point far from tributaries that could locally influence water quality. This point was located 6 km downstream of the MC section (31°42′–31°40'S; 60°29′–60°45'W) considered the control site where 85% of total discharge passes through (Drago, 1984). During the spatial samplings (2013–2016), vegetated littoral zones in the LTC were sampled when present. Macrophytes were classified according to Sculthorpe (1967) into five life forms (emergent, free floating, rooted floating stemmed, rooted floating leaved, and free submerged), and the relative percentage cover was assigned to each life form in the sampled macrophyte stands.

Depth (ultrasonic probe), pH, conductivity, temperature, and dissolved oxygen (HANNA checkers) were measured in situ. Subsurface water samples were collected by triplicate and transported on ice and in darkness to the laboratory. Turbidity (formazin turbidity units) was spectrophotometrically estimated at 450 nm wavelength with an HACH DR2000 spectrophotometer. A variable volume of water (300–1,200 ml) was filtered through Whatman GF/F glass-fibre filters. Filters were stored at −20 °C up to 3 weeks for the analysis of chlorophyll-*a* (a proxy of phytoplankton biomass). Chlorophyll-*a* was extracted from the filters with acetone (90%). Extracts were filtered, and their absorbances were measured at 750 and 664 nm and at 665 and 750 nm after acidification with HCl 0.1 M (APHA, 2005).

Total P (TP) was determined from unfiltered water by acid digestion followed by soluble reactive P (SRP) analysis by the ascorbic acid method (APHA, 2005). Filtered water samples were filtered again through Millipore filters (pore size: 0.45 μm) for the analysis of dissolved components. SRP was determined by the ascorbic acid method and chromophoric DOM (CDOM) by UV–Vis spectroscopy using a spectrophotometer HACH DR5000 and filtered Milli-Q water as baseline. Water colour (platinum–cobalt [Pt–Co], mg L^{-1}) was measured at 455 nm and considered as a surrogate measure of CDOM concentration. Absorbances at 250 nm (Abs_{250}) and 365 nm (Abs_{365}) were determined using quartz cuvettes with 1-cm-path length to estimate CDOM aromaticity from the equation proposed by Peuravuori and Pihlaja (1997): percentage of aromatic carbon ($\%C_{aro}$) = 52.509–6.780 × Abs_{250}/Abs_{365}. As the absorbance of the CDOM was assumed to be equal to zero above 700 nm, the absorbance at this wavelength was previously subtracted from absorbances at 250 and 365 nm to correct offsets (Kirk, 1994). During the temporal surveys (year 2012), samples were also analysed for determination of total dissolved P (DP) following the method described for TP and dissolved organic carbon (DOC) according to ISO (1999). Dissolved organic P was estimated as the difference between DP and SRP and particulate P (PP) as the difference between TP and DP. Samples were kept refrigerated until analysis within 24 hr after collection. When it was not possible to analyse samples within 24 hr after collection, they were frozen (P analysis) or acidified to a pH of less than two with phosphoric acid (DOC analysis).

Potential particle-bound alkaline phosphatase activity (APA) was estimated during the temporal surveys (year 2012). Suspended particles from 60 ml of water samples were collected on Whatman GF/F glass-fibre filters, which were then stored at −80 °C. Immediately before starting the enzyme assay, the filters were placed in centrifuge tubes with 5 ml of sodium carbonate–bicarbonate buffer (pH 10; Delory & King, 1945), sonicated for 45 s to release the particle-bound enzyme and centrifuged at 5,000 rpm for 3 min. The supernatant (2 ml) was transferred to test tubes and preincubated at 37 °C on an orbital shaker (200 rpm) for 5 min in darkness. The enzyme reaction started by adding 1 ml of a solution of p-nitrophenyl phosphate as substrate, magnesium chloriden to accelerate the reaction, and diethanolamine as pH buffer (final concentrations:

10 mM, 0.5 mM, and 1 M, respectively). Besides buffering pH, diethanolamine also activates the enzymatic reaction since it acts as acceptor of the released PO_4^{3-} (Berman, Wynne, & Kaplan, 1990). After 105 min of incubation under the same conditions, the p-nitrophenol concentration was measured spectrophotometrically at 410 nm. The absence of enzymatic activity provided by the filters was verified by treating Whatman GF/F glass-fibre filters without samples in the same way as the filters with samples. The potential APA (nmol p-nitrophenol formed L^{-1} h^{-1}) was normalized by chlorophyll-*a* (APA/Chl-*a*), although planktonic organisms other than phytoplankton also produce this enzyme (Wang et al., 2015).

Hydrometric level of the MC at the Paraná Harbour Gauge (HL) was provided by "Centro de Informaciones Meteorológicas". Water discharge (Q, m^3 s^{-1}) during 2012 was calculated following Toniolo (1999) as $Q = 7.6206 \times 2.71828183^{HL} + 2609.93 \times HL + 6288.27$. Loads (metric tons day^{-1}) of different P forms were estimated as the product of Q × P concentrations previously converted to appropriate units.

2.3 | Statistical analysis

Statistical analyses were conducted with PAST software (Hammer, Harper, & Ryan, 2001). Normality was checked with Kolmogorov–Smirnov test and homogeneity of variances with Bartlett test. Kruskal–Wallis with Dunn's posttest was used to assess differences among kinds of aquatic environments, as well as among vegetated and nonvegetated zones within LTC. Multiple linear regressions were applied to propose models for the explanation of temporal variability of SRP and TP concentrations in each environment and their loads in the MC (temporal samplings, year 2012) as well as for the explanation of the spatial variability of SRP and TP concentrations considering the sites sampled during the spatial samplings (2013–2016; dependent variables: P concentration and P load; independent variables: the other analysed limnological variables). In addition, multiple linear regressions were used to explain differences in SRP and TP concentrations among vegetated and nonvegetated zones within LTC using differences in other limnological variables (dependent variable: P concentration in nonvegetated zone–P concentration in vegetated zone; independent variables: value of each variable in nonvegetated zone–value of each variable in vegetated zone). Multiple linear regressions allow for identifying, among several independent variables, those that best contribute to explain the dependent variable. This analysis is adequate for the prediction of P dynamics, which is influenced by multiple variables, providing additional opportunities to increase the coefficient of determination (r^2) (Dimberg & Bryhn, 2015). For regression analysis, data were log transformed. All independent variables that were not collinear with each other were first included at the same time to explain the dependent variable. After that, the backward elimination approach was used (Hastie, Tibshirani, & Friedman, 2009). The overall significance of multiple regressions was tested using analysis of variance. Relations between differences of each limnological variable between vegetated and nonvegetated zones and the relative percentage cover of each macrophyte life form in sampled stands were assayed using Spearman analysis.

3 | RESULTS

3.1 | Temporal dynamics of P within the river-floodplain system

During the temporal samplings (year 2012), hydrological conditions changed from a low water phase (February–April) to a high water phase (May–August) and back to a low water phase (September–November; Table 1). The sediment peak arrived in the Paraná River between February and April, when the highest turbidity was observed (Figure 2). The high water phase coincided with minimum water temperatures and produced the connection of the LTC to the fluvial system.

The low water phase–sediment peak showed the lowest APA in the river and more connected environments (MC, SC, and LPC) but the highest APA in the more isolated site (LTC) (Table 1, Figure 2). The high water phase was characterized by increasing CDOM

TABLE 1 Mean values of limnological variables in the main channel and floodplain environments of the Middle Paraná River sampled during a low water phase-sediment peak (A, $n = 4$), flood (B, $n = 5$), and an ordinary low water phase (C, $n = 6$; February–November 2012)[a]

		Hyd. lev. m	Depth m	Turb. FTU	W. temp. °C	Cond. µS cm^{-1}	DO mg L^{-1}	pH	DOC µM	Colour mg L^{-1} Pt–Co	$\%C_{aro}$	Chl-*a* µg L^{-1}	APA nmol L^{-1} h^{-1}	APA/Chl-*a* nmol µg Chl-a^{-1} h^{-1}
MC	A	2.4 (0.1)		148 (48)	25.5 (1.6)	103 (3)	7.2 (1.3)	6.1 (0.3)	212 (5)	31 (7)	21 (3)	0.6 (0.0)	25 (5)	40 (7)
	B	3.0 (0.1)		37 (9)	17.5 (1.2)	75 (4)	7.2 (0.4)	6.8 (0.2)	283 (11)	46 (1)	23 (1)	1.1 (0.1)	34 (6)	33 (7)
	C	2.3 (0.3)		21 (3)	21.0 (0.9)	82 (7)	7.7 (0.7)	6.7 (0.4)	236 (12)	21 (3)	22 (1)	5.9 (1.0)	57 (9)	10 (2)
SC	A		2.8 (0.1)	94 (21)	24.1 (2.4)	105 (5)	5.8 (1.1)	6.4 (0.3)	224 (8)	23 (6)	16 (3)	14.2 (2.8)	32 (5)	3 (1)
	B		3.4 (0.2)	37 (9)	16.2 (1.6)	84 (4)	6.4 (0.4)	6.7 (0.2)	357 (25)	45 (2)	21 (1)	4.0 (0.8)	36 (4)	12 (3)
	C		2.4 (0.3)	21 (3)	19.9 (1.0)	123 (10)	6.4 (0.6)	6.5 (0.3)	394 (21)	17 (4)	18 (1)	22.4 (6.5)	61 (9)	6 (4)
LPC	A		1.5 (0.1)	140 (45)	24.4 (2.0)	103 (2)	7.0 (1.5)	6.5 (0.2)	205 (13)	22 (6)	14 (4)	2.0 (0.5)	24 (9)	13 (4)
	B		2.1 (0.1)	38 (8)	16.8 (1.4)	76 (4)	7.1 (0.4)	6.6 (0.1)	296 (9)	46 (2)	22 (1)	2.9 (0.7)	29 (3)	15 (4)
	C		1.3 (0.3)	26 (4)	20.6 (0.8)	77 (3)	7.8 (0.6)	6.6 (0.4)	247 (15)	19 (3)	22 (1)	7.1 (0.8)	48 (5)	7 (1)
LTC	A		0.2 (0.0)	176 (67)	23.3 (3.5)	83 (8)	5.1 (1.4)	6.9 (0.7)	969 (51)	71 (10)	15 (1)	19.6 (10.7)	99 (19)	8 (2)
	B		0.7 (0.1)	35 (8)	15.0 (1.6)	88 (3)	2.2 (0.7)	6.5 (0.2)	726 (127)	86 (13)	22 (1)	7.5 (2.0)	58 (16)	10 (3)
	C		0.4 (0.0)	43 (3)	17.8 (1.0)	63 (13)	0.5 (0.2)	6.2 (0.2)	1136 (119)	104 (7)	24 (1)	10.8 (2.9)	76 (19)	9 (3)

[a]Standard error is in parentheses. MC: main channel, SC: secondary channel, LPC: lake permanently connected to the fluvial system, LTC: lake temporarily connected to the fluvial system, Hyd. lev: hydrometric level of the MC, Turb.: turbidity, W. Temp.: water temperature, Cond.: conductivity, DO: dissolved oxygen, DOC: dissolved organic carbon, Chl-*a*: chlorophyll-*a*, $\%C_{aro}$: percentage of aromatic carbon of the chromophoric dissolved organic matter, APA: alkaline phosphatase activity associated to particles, APA/Chl-*a*: alkaline phosphatase activity associated to particles normalized by chlorophyll-*a*.

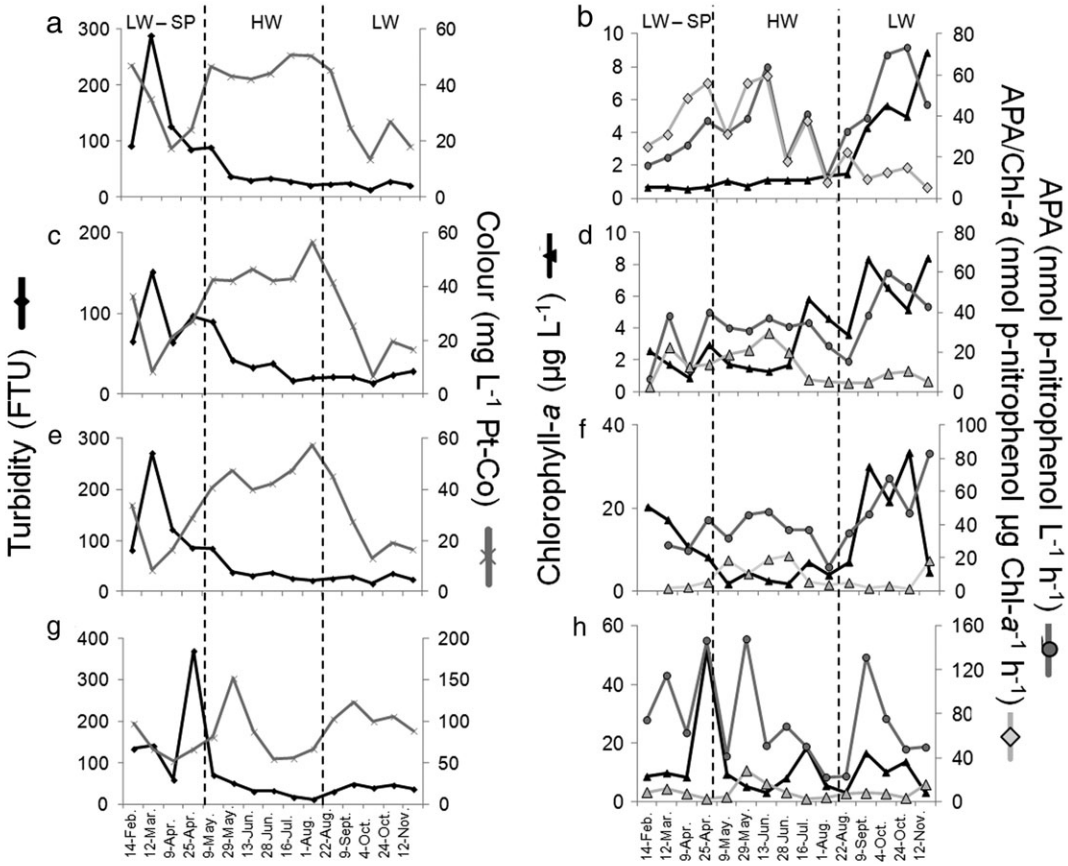

FIGURE 2 Variations in turbidity, colour, chlorophyll-*a*, alkaline phosphatase activity (APA), and APA/Chl-*a* at the main channel of the Middle Paraná River (a,b), the secondary channel (c,d), the lake permanently connected to the fluvial system (e,f), and the lake temporally connected to the fluvial system (g,h) sampled among February and November 2012. FTU = formazin turbidity units; HW = high waters; LW–SP = low waters–sediment peak; LW = low waters

aromaticity in all the sites and, only in the river and more connected environments, by increasing DOC and CDOM concentrations (Figure 2). This phase also showed a decrease in conductivity (MC, SC, and LPC), dissolved oxygen and chlorophyll-*a* (LTC). Finally, during ordinary low waters, chlorophyll-*a* and APA increased, whereas APA/Chl-*a* decreased in the fluvial system (Table 1, Figure 2).

Dissolved organic P represented a minor TP fraction in all the sites, with the lowest values during the low water phase–sediment peak (Figure 3). This phase showed the highest TP concentrations in the MC, SC, and LPC as well as the highest PT load within the MC due to an increase in PP. In the LTC, TP peaks occurred during all the hydrosedimentological phases (Figure 3) and were positively associated with DOC (multiple linear regression, $p < .05$) (Table 2). This site showed the highest variability in TP, with a relative difference between the lowest and the highest concentration of 680%, followed by the SC (500%), MC (460%), and LPC (190%). Turbidity explained TP concentration in the MC, SC, and LPC and TP load within the MC (multiple linear regression: $p < .001$, positive relations; Table 2). TP load was also explained by water level (multiple linear regression, $p < .05$, positive relation).

SRP concentration increased during high waters in the MC, SC, and LPC (Figure 3), similarly to SRP load in the MC (positive association with water level in the multiple linear regression, $p < .01$) (Table 2). In the LTC, SRP peaks occurred during high waters and the subsequent low water phase (Figure 3). This site showed the highest variability in SRP, with a relative difference between the lowest and the highest concentration of 1,150%, followed by the LPC (790%), SC (200%), and MC (130%). SRP concentration was positively associated with DOC in the MC and with CDOM in the SC and LTC (multiple linear regression, $p < .05$; Table 2). SRP was also related to chlorophyll-*a* and enzymatic activity. Its concentration was positively associated with APA/Chl-*a* and APA in the MC and the SC, respectively, whereas its load in the MC was positively associated with APA/Chl-*a* (multiple linear regressions, $p < .01$). Finally, temperature and chlorophyll-*a* explained SRP in the LPC (negative relations in the multiple linear regression, $p < .01$) (Table 2).

3.2 | Spatial dynamics of P within the river-floodplain system

CDOM concentration and pH presented low variability according to the kinds of aquatic environments studied during the spatial samplings (2013–2016; Table 3, Figure 4). Turbidity, dissolved oxygen, and CDOM aromaticity tended to decrease from the MC to the floodplain, whereas chlorophyll-*a* showed the opposite trend but without significant differences among types of aquatic environments (Kruskal–Wallis, $p > .05$).

Average TP concentration reached the lowest value in LPC and the highest one in LTC (Figure 4; 50% relative difference between both kinds of environments) without significant differences

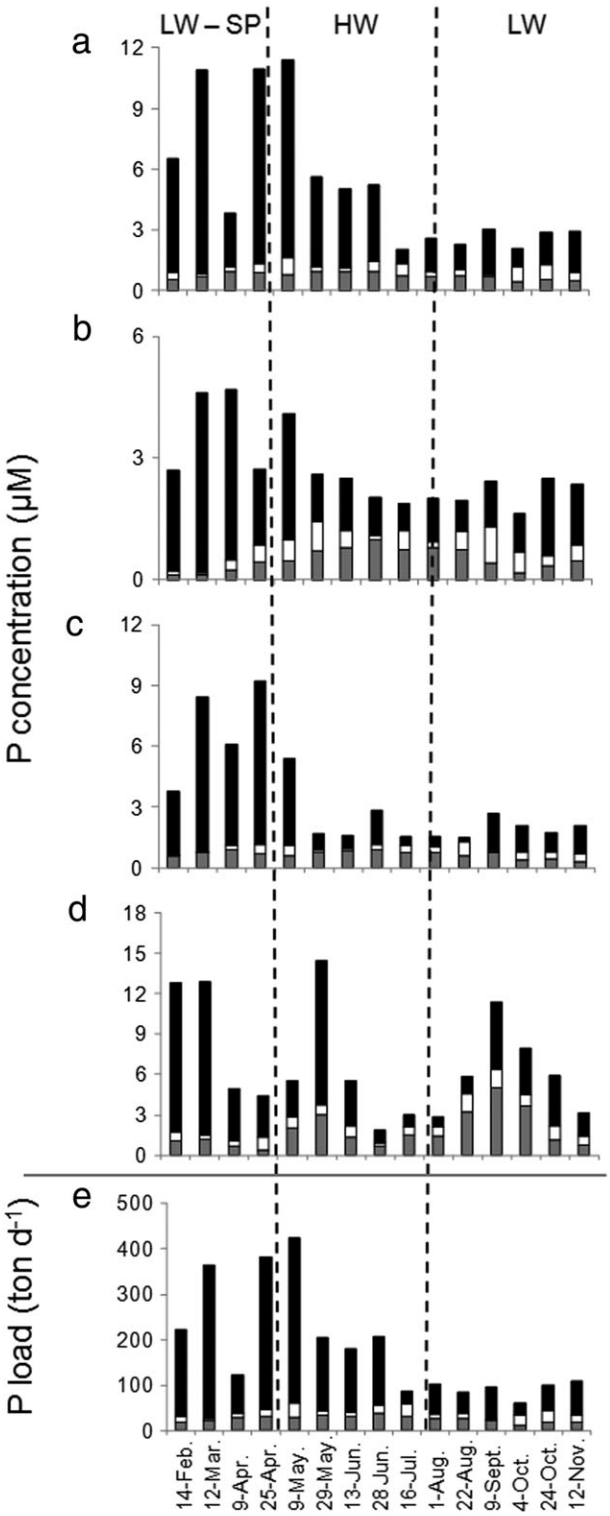

FIGURE 3 Variations in P concentrations at the (a) main channel of the Middle Paraná River, (b) the secondary channel, (c) the lake permanently connected to the fluvial system and (d) the lake temporally connected to the fluvial system sampled among February and November 2012, and (e) P load at the main channel. The sum of soluble reactive P (grey), dissolved organic P (white), and particulate P (black) represents total P. HW = high waters; LW = low waters; LW–SP = low waters–sediment peak; P = phosphorus

(Kruskal–Wallis, $p > .05$). Average SRP concentrations were less variable. The lowest value occurred in LTC and the highest one in the MC + AB (12% relative difference). Differences between the lowest and the highest TP and SRP concentrations were bigger considering each kind of aquatic environment (MC + AB: 1,020 and 2,030%, SC: 1,290 and 6,470%, LPC: 460 and 8,920%, LTC: 2,290 and 17,690%, respectively). Both TP and SRP concentrations were positively associated with turbidity ($p < .05$ and $p < .001$, respectively) and colour ($p < .001$) in the multiple linear regressions (Table 4).

3.3 | Variability of P concentration among vegetated and nonvegetated zones

The dominant life form in most macrophyte patches sampled during the spatial samplings (2013–2016) was the free floating (medium cover 59.7%), followed by the emergent (22.0%), the rooted floating leaved (11.1%), the rooted floating stemmed (7.0%), and the free submerged (0.2%). Average values of conductivity, pH, and CDOM concentration were similar in nonvegetated (126 µS cm^{-1}, 7.3, and 41 mg L^{-1} Pt–Co) and vegetated zones (125 µS cm^{-1}, 7.0, and 53 mg L^{-1} Pt–Co; Kruskal–Wallis, $p > .05$). Both zones showed differences in depth (average values in nonvegetated and vegetated zones: 1.5 and 0.8 m), turbidity (21 and 37 formazin turbidity units), dissolved oxygen (7.6 and 4.4 mg L^{-1}), and chlorophyll-*a* (14.8 and 16.3 µg L^{-1}; Kruskal–Wallis, $p < .05$).

Average concentrations of SRP and TP were, respectively, 30% and 50% higher in vegetated than in nonvegetated areas (Figure 5), with significant differences for TP (Kruskal–Wallis, $p < .05$; Figure 5). Differences in TP and SRP among both zones were positively related to differences in CDOM concentration evaluated through water colour (multiple linear regression, $p < .001$; Table 5). CDOM concentration was higher in vegetated than in nonvegetated zones, but patches with higher coverage of emergent macrophytes showed a larger increase in CDOM concentration (rho = 0.41, $p < .05$) and aromaticity (rho = 0.55, $p < .01$) (Spearman analysis). In addition, differences in SRP and chlorophyll-*a* between both zones were positively associated (multiple linear regression, $p < .05$; Table 5).

4 | DISCUSSION

P occurs as dissolved and particulate inorganic and organic forms. In the present study, P was mainly in particulate form, similarly to other turbid rivers (Almeida et al., 2015; Pedrozo & Bonetto, 1987). A substantial part of the PP carried by the Middle Paraná River is deposited in floodplain lakes during high waters (Maine et al., 2004). After that, PO_4^{3-} is released to the water column because the low pH and redox potential of bottom sediments favour the dissolution of calcium-bound P and iron-bound P, respectively, which represent a large fraction of PP (Maine et al., 2004; Carignan & Vaithiyanathan, 1999). PO_4^{3-} is able to form associations with DOM and Fe(III), which increase its permanence in the water column (Shaw et al., 2000). In this respect, variables linked to DOM were good predictors of SRP (a proxy of PO_4^{3-}), whereas TP was significantly explained by DOM and turbidity, as it will be discussed below.

TABLE 2 Results of linear regression models for the prediction of variability of TP and SRP concentrations in the main channel (MC) of the Middle Paraná River, a secondary channel (SC), a lake permanently connected to the fluvial system (LPC), and a lake temporarily connected to the fluvial system (LTC) as well as their loads in the MC[a]

	RC	SE	P	r^2
TP concentration				
MC				
$F = 19.66$, $p = <.001$, $r^2 = 0.62$				
Constant	−0.096	0.408	0.817	
Turbidity	0.477	0.108	<0.001	0.62
SC				
$F = 31.63$, $p < .001$, $r^2 = 0.72$				
Constant	0.233	0.190	0,244	
Turbidity	0.291	0.052	<0.001	0.72
LPC				
$F = 41.51$, $p < .001$, $r^2 = 0.78$				
Constant	−0.815	0.345	0.036	
Turbidity	0.578	0.090	<0.001	0.78
LTC				
$F = 9.61$, $p = .009$, $r^2 = 0.44$				
Constant	−3.347	1.690	0.071	
DOC	0.779	0.251	0.009	0.44
SRP concentration				
MC				
$F = 10.01$, $p = .0028$, $r^2 = 0.63$				
Constant	−1.363	0.673	0.066	
APA/Chl-*a*	0.094	0.025	0.003	0.44
DOC	0.291	0.121	0.033	0.18
SC				
$F = 33.66$, $p < .001$, $r^2 = 0.85$				
Constant	−0.900	0.159	<0.001	
Colour	0.278	0.036	<0.001	0.54
APA	0.104	0.021	<0.001	0.11
LPC				
$F = 9.12$, $p = .0039$, $r^2 = 0.60$				
Constant	1.415	0.299	<0.001	
Temperature	−0.222	0.092	0.032	0.06
Chlorophyll-*a*	−0.160	0.039	0.002	0.41
LTC				
$F = 10.84$, $p = .006$, $r^2 = 0.45$				
Constant	−3.131	1.242	0.026	
Colour	0.921	0.280	0.006	0.45
TP load				
MC				
$F = 5.25$, $p = .023$, $r^2 = 0.47$				
Constant	2.916	2.557	0.276	
Hydrometric level	3.771	1.704	0.047	0.16
Turbidity	0.723	0.276	0.022	0.25
SRP load				
MC				
$F = 13.70$, $p < .001$, $r^2 = 0.70$				
Constant	0.849	0.487	0.107	
APA/Chl-*a*	1.356	0.351	0.002	0.43
Hydrometric level	0.121	0.065	0.007	0.32

Note: APA = alkaline phosphatase activity; DOC = dissolved organic carbon; P = phosphorus; SRP = soluble reactive P; TP = total P.

[a]Period: February–November 2012 (n = 15). SE: standard error, RC: regression coefficient.

4.1 | Temporal dynamics of P

The hydrosedimentological regime regulates the functioning of river-floodplain systems by modifying material residence time and exchanges between environments (Ward et al., 2002). More isolated water bodies are particularly affected because they can function consecutively as swamps, lakes, and streams as the water level rises (Ward et al., 2002). This is consistent with the higher temporal variability of P in the LTC than in the MC and more connected environments.

In the fluvial system, TP load and concentration showed the highest values during the sediment peak (year 2012), which increased the PP input in the Paraná River. Sediment peaks occur during the late summer due to the arrival of the rainy season at the Andean headwaters of the Bermejo River, which provides the Paraná River with large quantities of suspended solids (Pedrozo & Bonetto, 1987). Since the LTC was disconnected from the fluvial system during the sediment peak, it did not receive inputs of solids from the Bermejo River. However, turbidity also increased in this lake, probably due to sediment resuspension and phytoplankton growth, processes occurring during low waters (Izaguirre, O'Farrell, & Tell, 2001; Maine et al., 2004). PP can be either contained within particles (Maine et al., 2004) or adsorbed on their surfaces (Müller et al., 2006). The positive relations of turbidity with TP concentration and load are explained by the positive effect of suspended particles on these variables.

We expected a decrease of TP load during high waters through increasing PP retention in floodplain lakes. Contrary to our hypothesis, the flood increased TP load in the MC. This could have been caused by increasing SRP load, as it was shown by the positive relations of both TP and SRP loads with the hydrometric level in the regression analysis. As previously pointed out, incoming PP from the river can quickly return to the water column, in the form of PO_4^{3-}, after sedimentation in lakes (Maine et al., 2004). In addition, floodplain soils can be SRP sources when inundated (Reavis & Haggard, 2016).

DOM concentration (principally the chromophoric fraction) was positively associated with SRP in the MC and floodplain environments. Floodplains can be CDOM sources, mainly during floods (Sieczko & Peduzzi, 2014), as it was suggested by increasing water colour in the river during high waters. Inputs of CDOM into the MC could have increased SRP load because CDOM can form associations with Fe(III) and PO_4^{3-}, decreasing the bioavailability of this anion and its sorption on surfaces (Shaw et al., 2000). Since CDOM favours PO_4^{3-} permanence in the water column, P could be largely exported from the floodplain as associated with CDOM. Similarly to the present study, Vinogradoff and Oliver (2015) found that predictive models of TP in Scottish lakes rich in organic matter were improved through the incorporation of a variable associated with DOM.

The increasing chlorophyll-*a* and APA in the MC, SC, and LPC during low waters (September–November 2012) were consistent with the hydrosedimentological conditions favourable for the development of planktonic organisms producing this enzime (Reynolds, 2006). The negative associations of chlorophyll-*a* and temperature with SRP in the LPC could have been caused by PO_4^{3-} consumption by phytoplankton, whose growth rate is higher in warmer waters (Reynolds, op. cit.). The positive associations of SRP with APA and APA/Chl-*a*

TABLE 3 Mean values of limnological variables in the main channel of the Middle Paraná River and large anabranches (MC + AB, n = 16), secondary channels (SC, n = 32), lakes permanently connected to the fluvial system (LPC, n = 28), and lakes temporarily connected to the fluvial system (LTC, n = 48)[a]

	Turb. (FTU)	Cond. (μS cm^{-1})	DO (mg L^{-1})	pH	Colour (mg L^{-1} Pt–Co)	%C_{aro}	Chl-a (μg L^{-1})
MC + AB	55 (13)	127 (26)	11.1 (3.7)	7.1 (0.1)	50 (5)	21 (1)	3.1 (0.5)
SC	44 (7)	149 (16)	9.0 (2.6)	6.9 (0.1)	51 (3)	20 (0)	4.9 (1.2)
LPC	36 (7)	147 (18)	6.0 (0.4)	6.9 (0.1)	49 (4)	20 (1)	4.1 (0.3)
LTC	38 (12)	113 (9)	5.7 (0.6)	7.0 (0.1)	51 (3)	17 (1)	13.8 (3.4)

Note: FTU = formazin turbidity units.

[a]Each site was sampled 4 times between 2013 and 2016. Standard error is in parentheses. Turb.: turbidity, Cond.: conductivity, DO: dissolved oxygen, %C_{aro}: percentage of aromatic carbon of the chromophoric dissolved organic matter, Chl-a: chlorophyll-a.

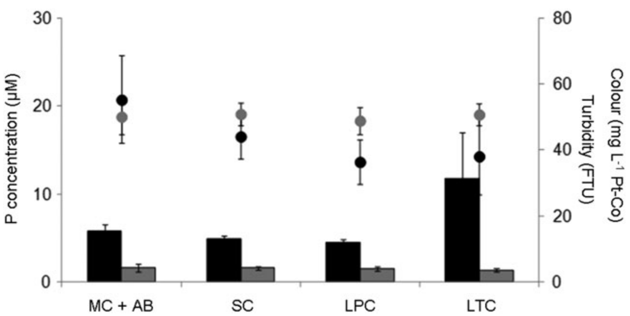

FIGURE 4 Mean values of total phosphorus (P) concentration (black bars), soluble reactive P concentration (grey bars), turbidity (black circles), and colour (grey circles) in the main channel of the Middle Paraná River and large anabranches (MC + AB; n = 16), secondary channels (SC; n = 32), lakes permanently connected to the fluvial system (LPC; n = 28) and lakes temporarily connected to the fluvial system (LTC; n = 48). Each site was sampled 4 times between 2013 and 2016. Vertical bars are standard errors. FTU = formazin turbidity units

TABLE 4 Results of linear regression models for the prediction of variability of TP and SRP concentrations considering 31 sites of the Middle Paraná River system (the main channel and three large anabranches, eight secondary channels, seven lakes permanently connected to the fluvial system, and 12 lakes temporarily connected to the fluvial system), each one sampled 4 times between 2013 and 2016 (N = 124)[a]

	RC	SE	P	r^2
TP concentration				
$F = 13.09$, $p < .001$, $r^2 = 0.19$				
Constant	−0.617	0.472	0.194	
Colour	0.513	0.113	<0.001	0.15
Turbidity	0.128	0.055	0.022	0.04
SRP concentration				
$F = 50.79$, $p < .001$, $r^2 = 0.47$				
Constant	−2.074	0.288	<0.001	
Colour	0.666	0.069	<0.001	0.43
Turbidity	0.094	0.034	0.006	0.04

Note: P = phosphorus; SRP = soluble reactive P; TP = total P.

[a]RC: regression coefficient, SE: standard error.

in lotic environments would indicate that, despite increasing concentration of this nutrient, its bioavailability could decrease (Rose & Axler, 1998). Similarly, SRP peaks occurred simultaneously to increasing enzymatic activity in the LTC. This is in accordance with the hypothesis proposed in the present study indicating an important contribution of CDOM-associated-PO_4^{3-} to the SRP pool. As it was pointed out, interactions between CDOM, PO_4^{3-}, and Fe(III) reduce P bioavailability by transformations of PO_4^{3-} to material of greater molecular size (Shaw et al., 2000).

4.2 | Patterns of P in relation to the kinds of aquatic environments

The positive relations of P with turbidity and colour considering the MC, AB, SC, LPC, and LTC sampled during 2013–2016 suggest that spatial patterns of P are also associated with suspended sediments and CDOM. The highest TP concentrations were observed in the most isolated environments, like in other river-floodplain systems (Roberto et al., 2009; Weilhoefer, Pan, & Eppard, 2008), whereas SRP concentrations were similar in the different kinds of environments.

Variability in P was higher considering each kind of aquatic environment in comparison with their variability among kinds of environments. Local conditions could determine inputs and outputs of sediments and CDOM into the water column as well as of associated P (Fergus, Soranno, Cheruvelil, & Bremigan, 2011). More isolated floodplain lakes are subject to local driving forces (e.g., ecological succession) during low waters (Thomaz, Bini, & Bozelli, 2007). Due to this, they follow distinct trajectories during large time periods. This is consistent with the higher variability of P considering LTC in comparison with more connected environments.

4.3 | Patterns of P in relation to aquatic vegetation cover

Floodplain vegetation can be a short-term P sink through absorption of this nutrient, which returns to the water column mainly during plant decay, and a long-term P sink due to burial of plant biomass (Barbieri & Esteves, 1991). Vegetation also favours the sedimentation of particles containing P by increasing floodplain roughness, which reduces current velocity (Altinakar, Kiedrzynska, & Magnuszewski, 2006). However, in the present study, turbidity and P were higher in vegetated than in nonvegetated zones of LTC. The highest turbidity of vegetated zones was probably associated with their location in shallower areas, which favours bottom sediment stirring through turbulence generated by the wind (Maine et al., 2004). Many macrophyte stands were composed of loosely disposed plants which allow the

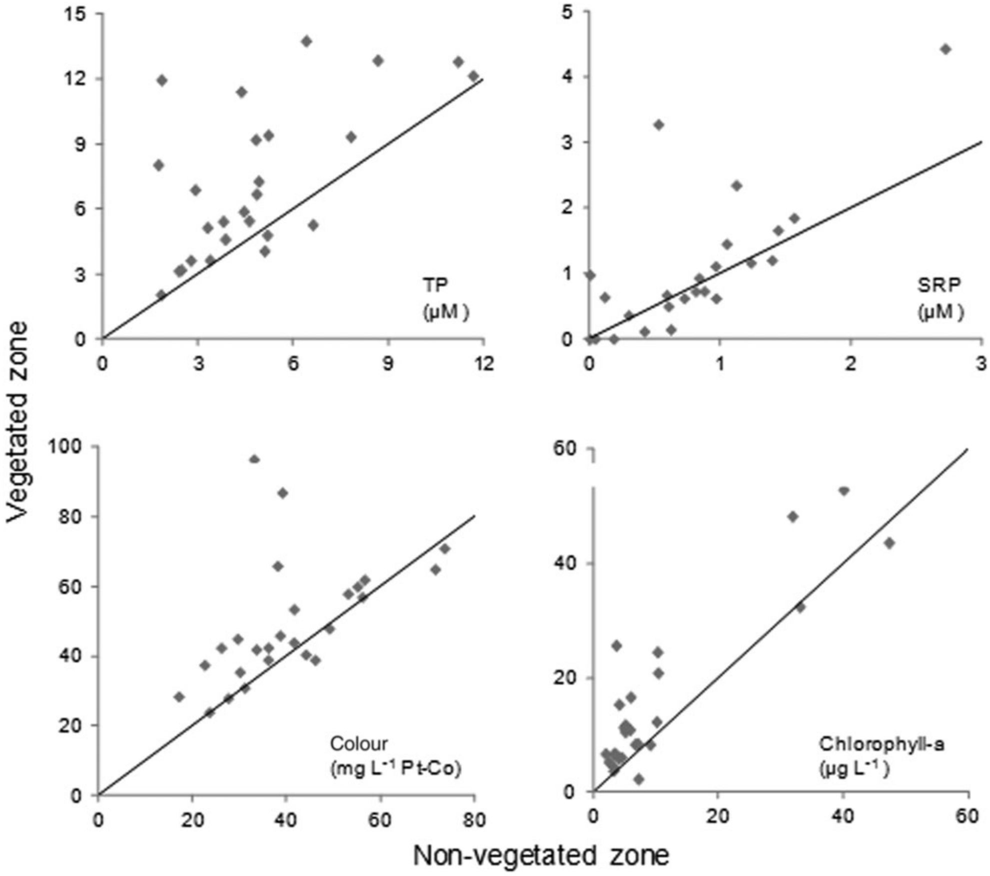

FIGURE 5 Relations among values of soluble reactive P (SRP), total P (TP), colour, and chlorophyll-*a* in nonvegetated and vegetated zones of lakes temporally connected to the fluvial system, which were sampled 4 times among 2013 and 2016. Dispersion points on the black line indicate that the value in both zones is the same, dispersion points above the black line indicate a higher value in the vegetated zone, and dispersion points below the black line indicate a higher value in the nonvegetated zone. P = phosphorus

TABLE 5 Results of linear regression models for the prediction of differences in TP and SRP concentrations among nonvegetated and vegetated zones of lakes temporarily connected to the fluvial system, each one sampled 4 times between 2013 and 2016 (N = 25, dependent variables: P concentration in nonvegetated zones–P concentration in vegetated zones)[a]

	RC	SE	P	r^2
Δ TP concentration				
F = 38.62, $p < .001$, $r^2 = 0.62$				
Constant	3.429	0.122	<0.001	
Δ Colour	0.191	0.030	<0.001	0.62
Δ SRP concentration				
F = 18.28, $p < .001$, $r^2 = 0.61$				
Constant	4.143	0.028	<0.001	
Δ Colour	0.010	0.002	<0.001	0.53
Δ Chlorophyll-*a*	0.015	0.007	0.032	0.14

Note: P = phosphorus; SRP = soluble reactive P; TP = total P.

[a]The predictor variables were the differences in values of other limnological variables among both zones (independent variables: value of each variable in nonvegetated zones–value of each variable in vegetated zones). RC: regression coefficient, SE: standard error.

wind to reach the water surface. In addition, wind acting in nonvegetated areas can produce waves that reach nearby vegetated zones.

Differences in P among vegetated and non-vegetated zones were positively related to differences in CDOM, suggesting that the effects of aquatic vegetation on P patterns were related to chemical conditions within patches. Although CDOM concentration tended to increase in vegetated zones, patches with higher coverage of emergent macrophytes showed higher CDOM increase compared with the adjacent nonvegetated area. The emergent macrophyte more frequently observed was *Ludwigia peploides* (Kunth) P.H. Raven (Schneider, pers. obs.). This macrophyte exudates more CDOM than free-floating ones (Gutierrez & Mayora, 2016). In addition to forming associations with P as previously discussed, CDOM could have decreased dissolved oxygen, which in turn favours P permanence in the water column (Maine et al., 2004). On the other hand, rooted macrophytes take up P from bottom sediments, operating as "P pumps" to the water column through exudates and lixiviates (Barbieri & Esteves, 1991). The results suggest that the effects of macrophytes on P dynamics depend on the abundance of emergent species (even when this life form is not dominant) because they generate favourable conditions for P permanence in the aquatic environment.

5 | CONCLUSIONS

The present study suggests that, despite being a "trap" for particle-bound P carried by the river, the floodplain is a net source of this nutrient through the release of the dissolved fraction. DP could be largely exported during floods as associated with DOM. Furthermore, the effect of aquatic macrophytes on P spatial patterns seems to be influenced by CDOM exudation. Taking into account these conclusions, DOM should be considered to analyse P dynamics in river-floodplain systems.

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