



## PHYTOPLANKTON FUNCTIONAL GROUPS DRIVEN BY ALTERNATIVE STATES IN A TROPICAL FLOODPLAIN LAKE (PANTANAL, BRAZIL)

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**Abstract:** The flood pulse associated with local factors is the main drivers of the phytoplankton functional groups. The aim of this study was to evaluate the dynamics of the phytoplankton community and the Reynolds Functional Groups (RFG) and their relationships with the alternative states in a Pantanal floodplain lake. The Coqueiro Lake (municipality of Poconé, state of Mato Grosso, Brazil) was sampled monthly at three sites from April 2002 to May 2003. Three periods were identified: i) period I (first receding) with colonization of *Egeria najas* (Alismatales, Hydrocharitaceae), reduced depths and clear waters, characterized by the lowest species richness (mean = 23 taxa/sample) and reduced phytoplankton biomass (mean = 1.0 mg L<sup>-1</sup>); ii) periods II (low waters and rising) without *Egeria najas*, with lowest influence from the river, lowest depths, turbid waters, highest phytoplankton biomass (mean = 9.8 mg L<sup>-1</sup>) and species richness (mean = 29 taxa/sample); iii) periods III (high waters and beginning of the second receding) with *Egeria najas* and high influence from the river, greater depths, clear waters, with intermediate species richness (mean = 26 taxa/sample) and lowest phytoplankton biomass (mean = 0.7 mg L<sup>-1</sup>). Phytoplankton was composed mainly of nanoplanktonic algae with greatest contributions in the low waters without *Egeria najas* and was represented by 16 RFG, with reduced variability between the three periods and sites. The functional groups K, P, F, J, H1 and H2 were important in this shallow flood lake governed by natural mechanisms of alternation of clear water regime with reduced phytoplankton biomass to a new state of turbid water dominated by phytoplankton. The variations in the phytoplankton functional groups were related to the physical and chemical regime of the lake and the hydrodynamics of the flood system, which acts as a continuous renewal of the habitat conditions in the different alternative states the lake.

**Keywords:** microalgae; shallow lakes; wetland.

### INTRODUCTION

River hydrodynamics in floodplains subjects the many shallow lakes of these regions to water level fluctuations and to the flow of matter and energy (Junk *et al.* 1989, 2011, Junk & Wantzen 2006)

where phytoplankton dynamics is as variable as the seasonal patterns of flooding and isolation (Townsend 2006). Considering these aspects, the classic concept of habitat model (Southwood 1977) has been applied to phytoplankton, based on a number of diagnostic environmental axes,

which distinguish attributes and adaptations of the species that make up the pelagic vegetation (Padisák *et al.* 2009, Brasil & Huszar 2011).

According to the complexity of these macrosystems, some shallow lakes are eutrophic and may change “abruptly” alternating from a macrophyte-dominated state of clear waters to a new state of turbid waters, dominated by phytoplankton (Scheffer 1993, Scheffer & Carpenter 2003, 2007). The sharp transitions between a clear macrophyte-dominated state and a turbid state without submerged plants also occur in the tropical floodplain lake, albeit driven by a largely different set of mechanisms. Contrary to what is found in temperate lakes there is no evidence for top-down control of phytoplankton biomass associated with the macrophyte-dominated state in a tropical lake (Loverde-Oliveira *et al.* 2009).

Studies have analyzed phytoplankton in shallow lakes governed by natural mechanisms driving regime alternation (O’Farrell *et al.* 2011, Izaguirre *et al.* 2012, Tezanos-Pinto & O’Farrell 2014, Bertani *et al.* 2016, Gamito *et al.* 2019) and applied the approach of functional groups in systems with alternative states (Loverde-Oliveira 2005, Tezanos-Pinto *et al.* 2015). The studies using the functional groups to analyze the phytoplankton variation and the driving factors have been efficient in several floodplain lakes for example in the Paraná River (Devercelli 2006, Devercelli *et al.* 2014, Bortolini *et al.* 2016), Pantanal (Loverde-Oliveira & Huszar 2007), Araguaia River (Nabout *et al.* 2006, Nabout & Nogueira 2007) and Amazonian basin (Alves 2011, Lobo *et al.* 2018).

The objective of this study was to evaluate the dynamics of the phytoplankton community and the Reynolds Functional Groups (RFG) and their relationships with the alternative states in a Pantanal floodplain lake. We tested the hypothesis that the flood pulse represents a macro-factor that regulates the phytoplankton biomass and composition expressed by the RFG in the studied ecosystem.

## MATERIAL AND METHODS

### *Study area*

The study was conducted in Coqueiro Lake in the Pantanal of Poconé (16°15’12” S, 56°22’12” W; SIRGAS 2000), state of Mato Grosso, Brazil,

belonging to the floodplain of the Cuiabá River (Figure 1). It is a shallow, elongated, polymictic and eutrophic. During the high-water period, has clear waters and is characterized by the colonization of *Egeria najas* Planch. (Alismatales, Hydrocharitaceae) and by populations of *Eichhornia azurea* Kunth (Commelinales, Pontederiaceae) and *Eichhornia crassipes* (Mart.) Solms (Commelinales, Pontederiaceae) in the littoral zone (Loverde-Oliveira *et al.* 2009).

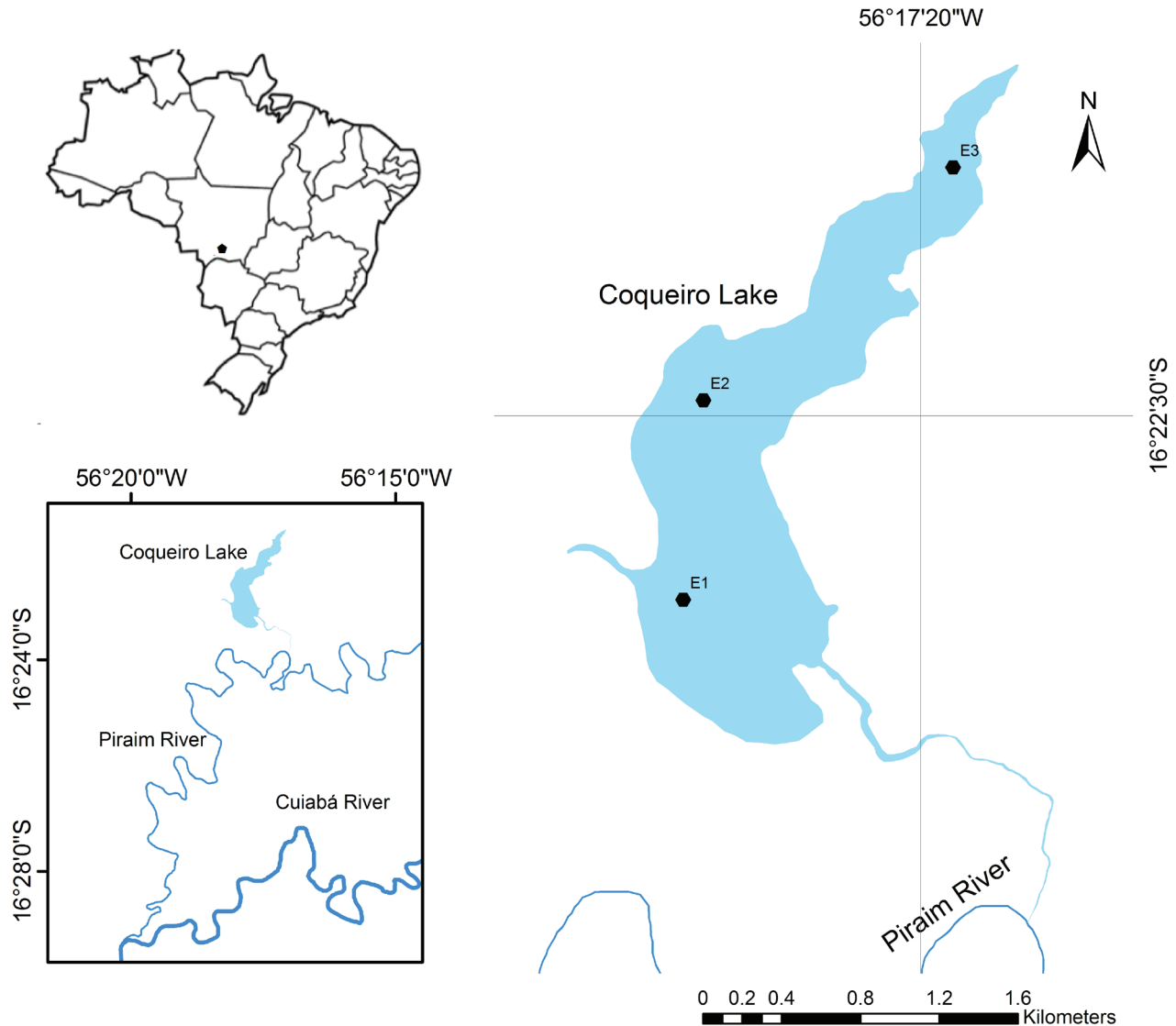
The climate of the region is hot and humid (Koeppen Aw), with dry winter and rainy summer. The average historical temperature ranges from 24°C to 26°C, with historical annual total rainfall of 1,000 - 1,600 mm (Alvares *et al.* 2014).

### *Sampling and sample analyses*

Monthly samples were taken from April 2002 to May 2003 at three sites (Figure 1): E1, located in the limnetic region under the influence of a channel (*Corixo*) that connects the Coqueiro Lake to the Piraim River, in the flood; E2, located in the limnetic and deeper region of the lake; and E3, in the littoral zone next to a stand of emergent aquatic macrophytes and under the influence of a temporary channel. For analyses of the phytoplankton and the environmental variables, water samples were collected under the water surface, simultaneously. Quantitative samples of phytoplankton were fixed with Lugol acetic solution.

The densities of phytoplankton (ind mL<sup>-1</sup>) were estimated in random fields (Uehlinger 1964) according to the sedimentation method (Utermöhl 1958). Phytoplankton biovolume (mg L<sup>-1</sup>) was estimated as the product of population density by the mean volume of each species (Hillebrand *et al.* 1999). Phytoplankton taxa were grouped according to the Reynolds Functional Groups (Reynolds *et al.* 2002, Padisák *et al.* 2009, Kruk *et al.* 2017) for species that contributed on average with more than 4% to the total biomass. The taxonomic diversity of phytoplankton was calculated using richness (*i.e.*, species per sample), Shannon and Wiener diversity index (Shannon & Weaver 1963), and evenness (Pielou 1966) of species.

Meteorological data were provided by Padre Ricardo Remetter Meteorological Station, about 80 km in a straight line from the lake. The water temperature, electrical conductivity, pH and dissolved oxygen were determined using a Mettler



**Figure 1.** Location of the Coqueiro Lake, Cuiabá River Basin, state of Mato Grosso, Brazil, showing the sampling sites.

Toledo meter; alkalinity according to Golterman *et al.* (1978) and Mackereth *et al.* (1978); the concentrations of  $\text{CO}_2$  based on Carmouze (1994); turbidity with HACH 2100P portable turbidimeter, color by direct reading (Nessler-Quanti 200), suspended material according to Teixeira *et al.* (1965); the depth of the lake ( $Z_{\text{max}}$ , m), water transparency (m) was obtained using a Secchi disk, and the euphotic zone ( $Z_{\text{eu}}$ , m) was calculated as 2.7 times the depth of the Secchi disk (Cole 1994); total nitrogen (TN), total phosphorus (TP), ammonium ( $\text{N-NH}_4^+$ ), nitrate ( $\text{N-NO}_3^-$ ), soluble reactive phosphorus (SRP) and soluble reactive silica (SRSi), based on Golterman *et al.* (1978). Chlorophyll-*a* was analyzed using the method of Nusch & Palme (1975).

#### Data analyses

The TN:TP, Si  $\text{SO}_3^-$ :P  $\text{PO}_4^{3-}$  and Si  $\text{SO}_3^-$ :NID were calculated by atomic ratio. Approximations of the limitation of phytoplankton growth by nutrients, related to the taxonomic groups, were made comparing the semi-saturation ( $K_m$ ) constants with the nutrient concentrations of the Coqueiro Lake (Sommer 1989). The dissolved inorganic nutrients and the  $K_m$  values of literature were used according to Huszar & Caraco (1998). The percentage of limitation was calculated as  $\% \text{ limitation} = 100 * [1 - (C_i / C_i + K_m)]$ , where  $K_m$  is the median value for the different taxonomic groups and  $C_i$  is the concentration of the inorganic nutrient in sample *i*.

To order the environmental variability and to

determine spatial and temporal changes in the physical and chemical conditions of the lake, the Principal Components Analysis (PCA) was performed from the following descriptor variables: water temperature,  $z_{eu}$ ,  $z_{max}$ , suspended matter, turbidity, dissolved oxygen, pH, CO<sub>2</sub>, alkalinity, electrical conductivity, N NH<sub>4</sub><sup>+</sup>, N NO<sub>3</sub><sup>-</sup>, SRP, SRSi, NT, PT, chlorophyll *a* (CANOCO 4.0; Ter Braak 1986). The significance of the four axes and the variables was obtained through the Monte Carlo permutation test (199 non-restrictive permutations,  $p < 0.05$ ) from transformed data. The averages of the biotic and abiotic variables of the water were compared through unidirectional Analysis of Variance (ANOVA) considering the sampling stations and periods of the hydrological cycle ( $p < 0.05$ ). To determine how much of the variance of the phytoplankton (RGF) was explained from the environmental variables, a Redundancy Analysis (RDA) was performed. Before performing the RDA, we avoided the multicollinearity of the abiotic variables excluding those with an inflation factor (FVI) greater than 10. In relation to the biotic data (RGF), they were previously transformed by the Hellinger method using the “decostand” function of the Vegan package (Oksanen *et al.* 2019). In addition, in order to obtain the most important variables, we performed a forward selection using the “ordistep” function (R Core Team 2018).

## RESULTS

### *Environmental variability*

In the study period, the total annual precipitation (1,259 mm) was within the climatological patterns of the region, when compared with the historical averages (800-1,600 mm). Precipitations on average presented maximum values in period II and the minimum in period I (Table 1).

The first two PCA axes explained 50% of the total variability of the data, showing the occurrence of three periods: period I (4/16 to 7/21/2002); first receding; period II (02/08/2002 to 01/31/2003), low waters and includes the beginning of the rising; and period III (10/02 to 05/31/2003) of high waters and beginning of the second receding. The periods I and III had the greatest depths, waters and euphoric zone, clear waters, lowest richness and lowest phytoplankton biomass, with lowest concentrations of nutrients, suspended matter, highest values of

CO<sub>2</sub>, alkalinity and electrical conductivity; the period II (low water) had lowest fluvial influence, lower maximum depths and the euphotic zone, turbid waters, highest biomass and species richness, and highest concentrations of phosphorus, ammonium and chlorophyll-*a* (Table 1).

### *Phytoplankton Community and Functional Groups (RFG)*

A total of 140 phytoplankton species were identified, distributed in 10 taxonomic classes: Chlorophyceae (N = 39 species), Zygnemaphyceae (N = 29), Cyanobacteria (N = 28), Bacillariophyceae (N = 23), Euglenophyceae (N = 8), Chrysophyceae (N = 6), Chryptophyceae (N = 3), Dinophyceae (N = 2) and Oedogoniophyceae and Rhodophyceae with one species each. A total of 16 RFG was recognized throughout the study, composed especially of nanoplanktonic algae with greatest contributions in the low water period.

The period I was marked by the expressive colonization of *Egeria najas*, and reduced phytoplanktonic biomasses in the three sampling sites, varying on average from 0.9 to 1.2 mg L<sup>-1</sup>, intermediate values, when compared with other periods, of specific richness (mean = 23 taxa/sample) and diversity (mean = 2.8 bits ind<sup>-1</sup>). Evenness ranged from 36 to 83% and indicated a significant variability in the contribution of species in biomass for the whole, with no marked dominance of species (Figure 2). The site E1 was characterized by the dominance of zygneaphyceans of the functional group P at the beginning of the period, followed by cyanobacteria, mainly colonial small-cell coccoids functional group K (Figure 3). In turn, at E2, there was dominance of centric diatoms of the functional group P accompanied by coccoid cyanobacteria of the functional group K. It is worth noting the occurrence in the three sites of the functional group A, exclusive of this period. E3 was more similar to the E2 site, but with more expressive contributions of nanoplanktonic cromulinales, chrysophyceae of the functional group X3 (Figure 3; Supplementary Material 1). Sites E1 and E2 were marked by the dominance of the nano (< 20 μm) and microplankton (20-50 μm), but the littoral zone (E3) also showed significant contributions of the fraction larger than 50 μm (Figure 3). The period II, without *Egeria najas*, was characterized by high phytoplanktonic biomass (mean = 9.8 mg L<sup>-1</sup>,  $p < 0.0001$ ), with very significant

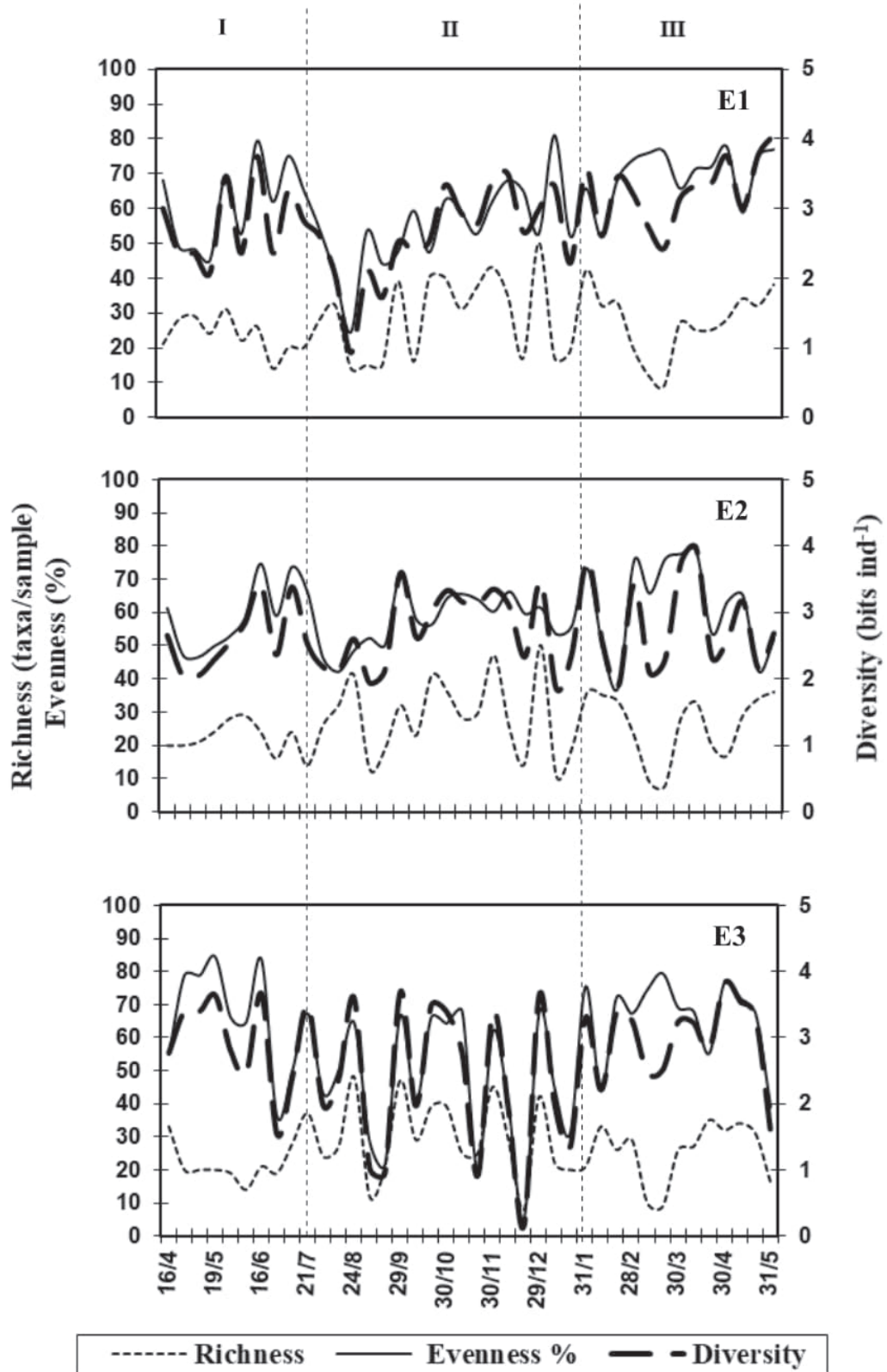
**Table 1.** Annual mean values of the variables per site (E1, E2, E3) and collection periods of receding (PI), low waters and beginning of the rising (PII), end of the flood, high waters and second receding (PIII), in Coqueiro Lake, municipality of Poconé, state of Mato Grosso, Brazil.

Variables	E1	E2	E3	PI	PII	PIII
Precipitation (mm)	-	-	-	23.85	869.5	463.8
Water temperature (°C)	27.9	27.7	27.7	26.4	28.5	28.1
Maximum depth (m)	1.5	1.6	1.2	1.5	1	1.9
Water transparency (m)	0.9	0.9	1	1	0.4	1.4
Euphotic zone (m)	1.5	1.5	1.2	1.5	1	1.9
Suspended material (mg L <sup>-1</sup> )	51	39	36	42	51	31
Turbidity (NTU)	28	30	17	26	37	8
Color (mg L <sup>-1 Pt</sup> )	67	75	76	64	107	43
Electrical conductivity (µS cm <sup>-1</sup> )	30	26	22	26	23	30
pH	5.9	6.3	5.4	5.8	6.2	5.4
Alkalinity (mg CaCO <sub>3</sub> L <sup>-1</sup> )	15	12	10	14	9	15
CO <sub>2</sub> (µ Mol L <sup>-1</sup> )	28	27	49	31	18	60
Dissolved oxygen (%)	41	41	13	21	37	37
NT (µg L <sup>-1</sup> )	458	537	515	701	610	162
PT (µg L <sup>-1</sup> )	222	309	190	204	283	223
N NH <sub>4</sub> <sup>+</sup> (µg L <sup>-1</sup> )	58	52	105	63	98	42
N NO <sub>3</sub> <sup>-</sup> (µg L <sup>-1</sup> )	37	59	37	66	30	41
NID (µg L <sup>-1</sup> )	94	111	142	130	128	83
P PO <sub>4</sub> <sup>3-</sup> (µg L <sup>-1</sup> )	42	46	32	41	61	13
Si SO <sub>3</sub> <sup>-</sup> (µg L <sup>-1</sup> )	186	168	170	436	79	41
TN:TP (atomic)	6	6	8	14	5	2
Si SiO <sub>3</sub> <sup>-</sup> :P PO <sub>4</sub> <sup>3-</sup> (atomic)	5	5	6	12	2	4
Si SiO <sub>3</sub> <sup>-</sup> :NID (atomic)	1	0.8	0.6	1.7	0.03	0.3
Chlorophyll -a (µg L <sup>-1</sup> )	26	24	16	16	39	6

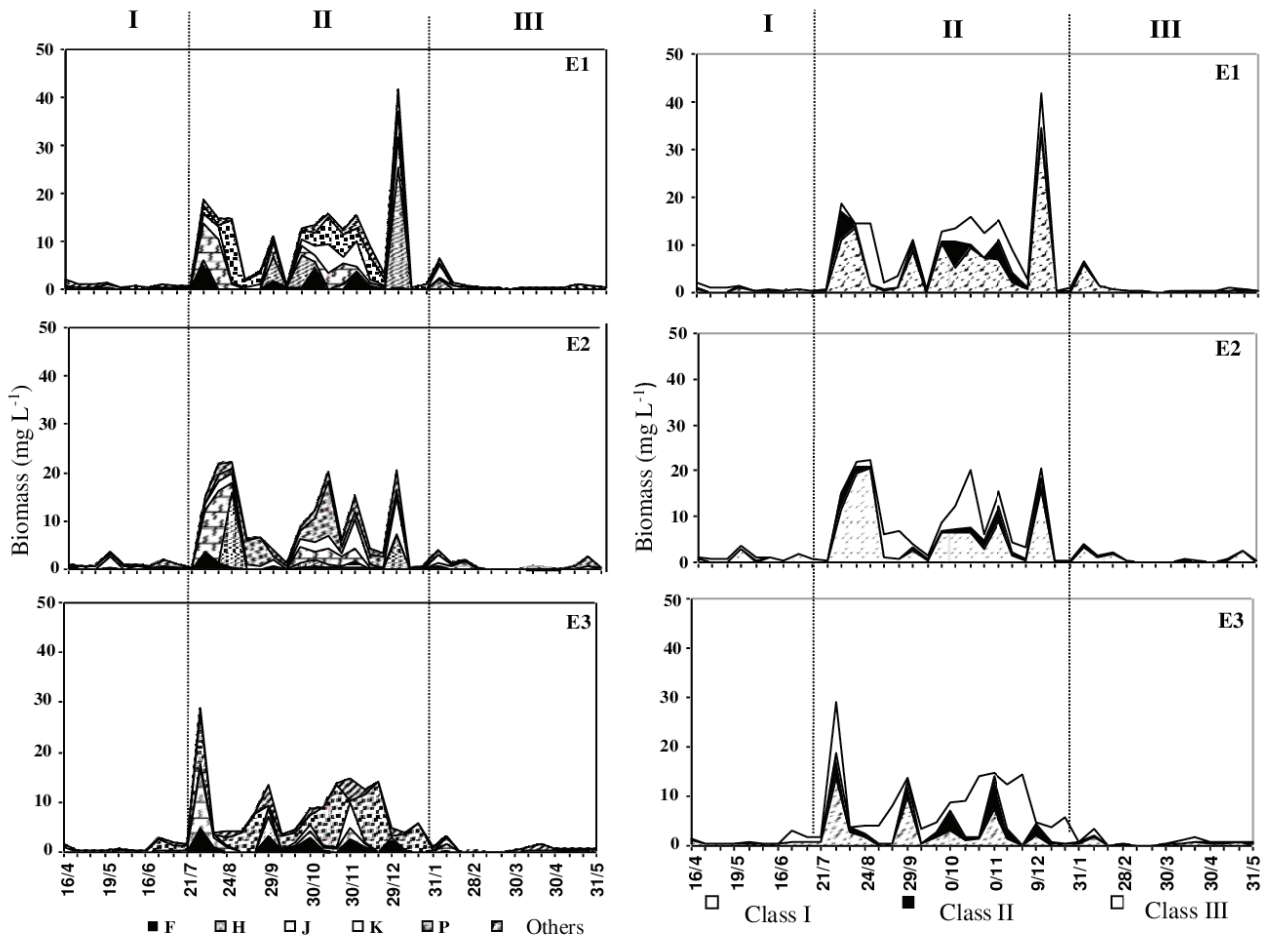
temporal variability, highest specific richness (mean = 29 taxa/sample;  $p < 0.0001$ ) and lowest diversity (mean = 2.5 bits ind<sup>-1</sup>;  $p < 0.0001$ ), when compared with the other periods. The high variability of evenness (4 to 81%) indicated that also in this period, there was no marked dominance (Figure 2). The limnetic site (E1) was characterized by the dominance of diatoms of the functional group P and filamentous cyanobacteria of the functional groups H1 and H2, besides cyanobacteria of the functional group K, followed by chlorophyceans of the functional groups J and F (Figure 3). In E2 and E3, there was dominance of centric diatoms of the functional group P, accompanied by chlorophyceans of the functional group J) and coccoid cyanobacteria of the functional group K (Figure 3; Supplementary Material 1).

The period III, high water and second

receding, was again colonized by *Egeria najas* and characterized by reduced phytoplanktonic biomass (mean = 0.7 mg L<sup>-1</sup>), with intermediate specific richness (mean = 26 taxa/sample) and greater diversity (mean = 3.2 bits ind<sup>-1</sup>) when compared with the other periods. The evenness of 37-79% indicated that also in period III there was an expressive variability in the contribution of the species to the whole, with no marked dominance (Figure 2). The limnetic sites did not differ markedly and were dominated at the beginning of period III by coccoid cyanobacteria of the functional group K and F, as well as filaments of the functional group S, followed by colonial coccoid chlorophyceans of the functional groups F and J and flagellates of functional groups X<sub>3</sub>, W<sub>1</sub> and Y (Figure 3). The littoral site in period III presented the greatest variability among the dominant groups. Initially, it was better represented



**Figure 2.** Variations in diversity, richness and evenness of phytoplankton species at the surface of the three sites (E1, E2, E3) in Coqueiro Lake, municipality of Poconé, state of Mato Grosso, Brazil, in the periods of receding (I), low waters and beginning of the rising (II), end of the flood, high waters and second receding (III).



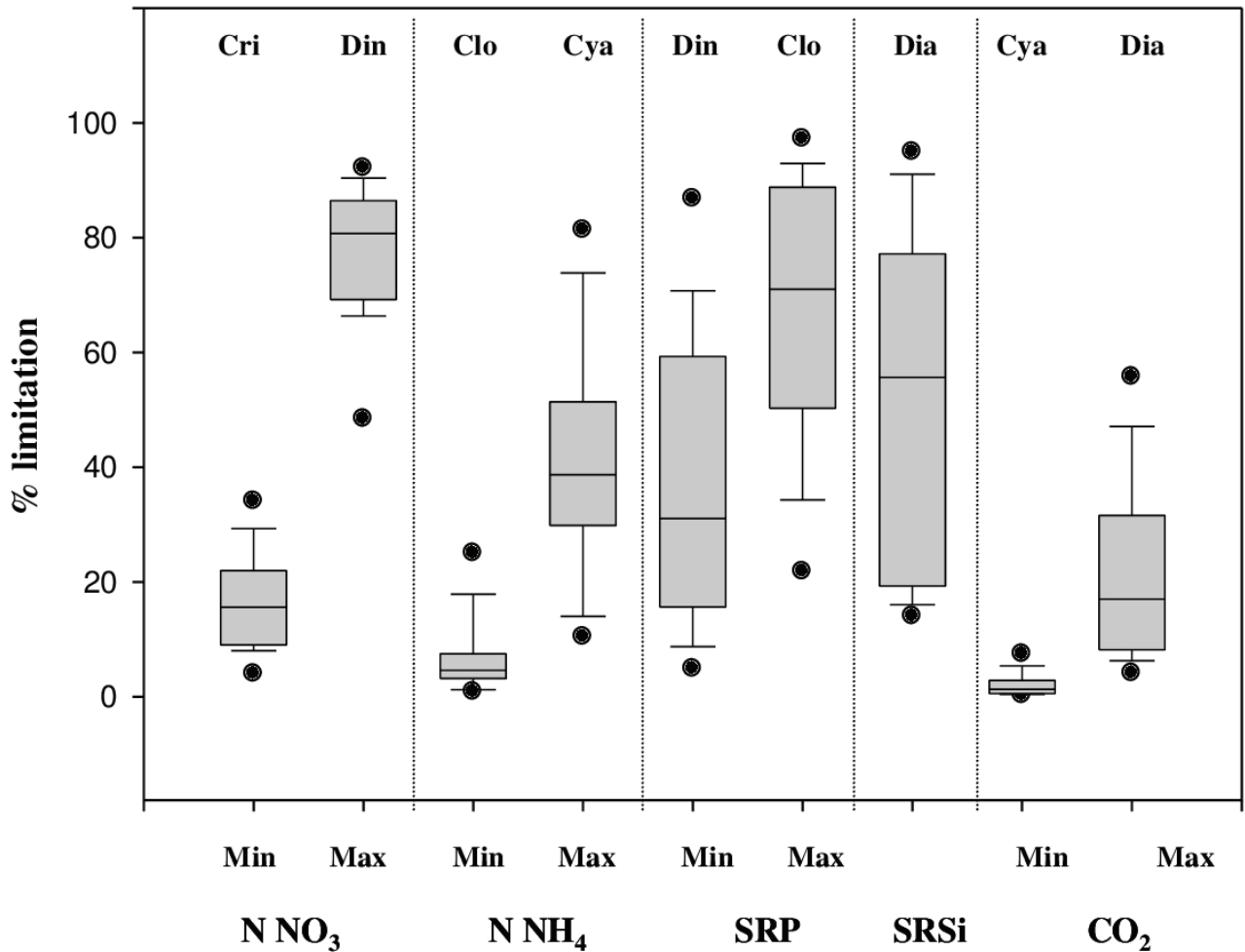
**Figure 3.** Variations in biomass per functional group and size class of phytoplankton, at the surface of the three sites (E1, E2, E3), in Coqueiro Lake, municipality of Poconé, state of Mato Grosso, Brazil, in the periods of receding (I), low waters and beginning of the rising (II), end of the flood, high waters and second receding (III). Class I:  $<20\mu\text{m}$ ; class II:  $20\text{--}50\mu\text{m}$ ; Class III:  $>50\mu\text{m}$ .

by coccoid cyanobacteria of the functional group K, followed by chlorophytes of functional groups E, J and  $X_1$  (Figure 3). At this site, there were also contributions from nanoplankton chromulinales of the functional group  $X_3$  and of the functional group Y (Supplementary Material 1). Higher contributions of zygnephyceans were found when compared with the other sites, represented by the functional group T and TD. Nano ( $<20\mu\text{m}$ ) and microplankton ( $20\text{--}50\mu\text{m}$ ) fractions dominated at the three sampling sites. At the beginning of period III, the littoral site (E3) was dominated by fractions  $>50\mu\text{m}$  (Figure 3).

When comparing nutrient limitation using phytoplankton groups (Figure 4), three patterns emerge: in the first ( $\text{CO}_2$  and  $\text{N-NH}_4$ ), all large groups are not strongly limited; in the second ( $\text{N-NO}_3$ ), there could be large differences between the groups, with limitation only for the group with greater  $K_m$  (dinoflagellates); and in the third (SRSi and SRP),

there could be limitation at intermediate levels and with great variability for any taxonomic group. The second pattern could lead to a high selection of species in different taxonomic groups. When the first pattern dominates, it is not expected that dissolved nutrients play a key role in the selection of phytoplankton groups. The data of the present study based on  $K_m$  values suggest, therefore, an expressive selective potential for  $\text{N-NO}_3$ , intermediate potential for SRP and SRSi and low selective potential for  $\text{CO}_2$  and  $\text{N-NH}_4$ , for the different phytoplankton groups (Figure 4).

In RDA 21% of the data variance was explained ( $F_{5,36} = 2,57, p = 0.001$ ). The spatial and temporal gradient was observed in the first axis that was influenced by Turb ( $-0.85$ ),  $\text{CO}_2$  ( $0.70$ ), and  $\text{TN:TP}$  ( $0.32$ ). The second axis was influenced by  $\text{NNO}_3$  ( $-0.69$ ) and  $\text{NNH}_4$  ( $0.61$ ). This analysis evidenced high similarity spatial and temporal of the phytoplankton, with the



**Figure 4.** Box plot of the percentage of limitation to phytoplankton growth, based on the semi-saturation constants ( $K_m$ ) in Coqueiro Lake, municipality of Poconé, state of Mato Grosso, Brazil. For all nutrients, except for silica, the groups with lower (Min) and higher (Max)  $K_m$  were considered. Initials of taxonomic groups: Cri - chrysophyceans; Din - dinoflagellates; Clo - chlorophyceans; Cya - cyanobacteria; Dia - diatoms. The line inside the boxes is the median, while the boundaries of the boxes, dashes and points cover 75%, 90% and 95% of the data, respectively.

discrimination the majority of RFGs in the first axis and only of the RFGs F, T and H1 in the second axis (Figure 5).

### DISCUSSION

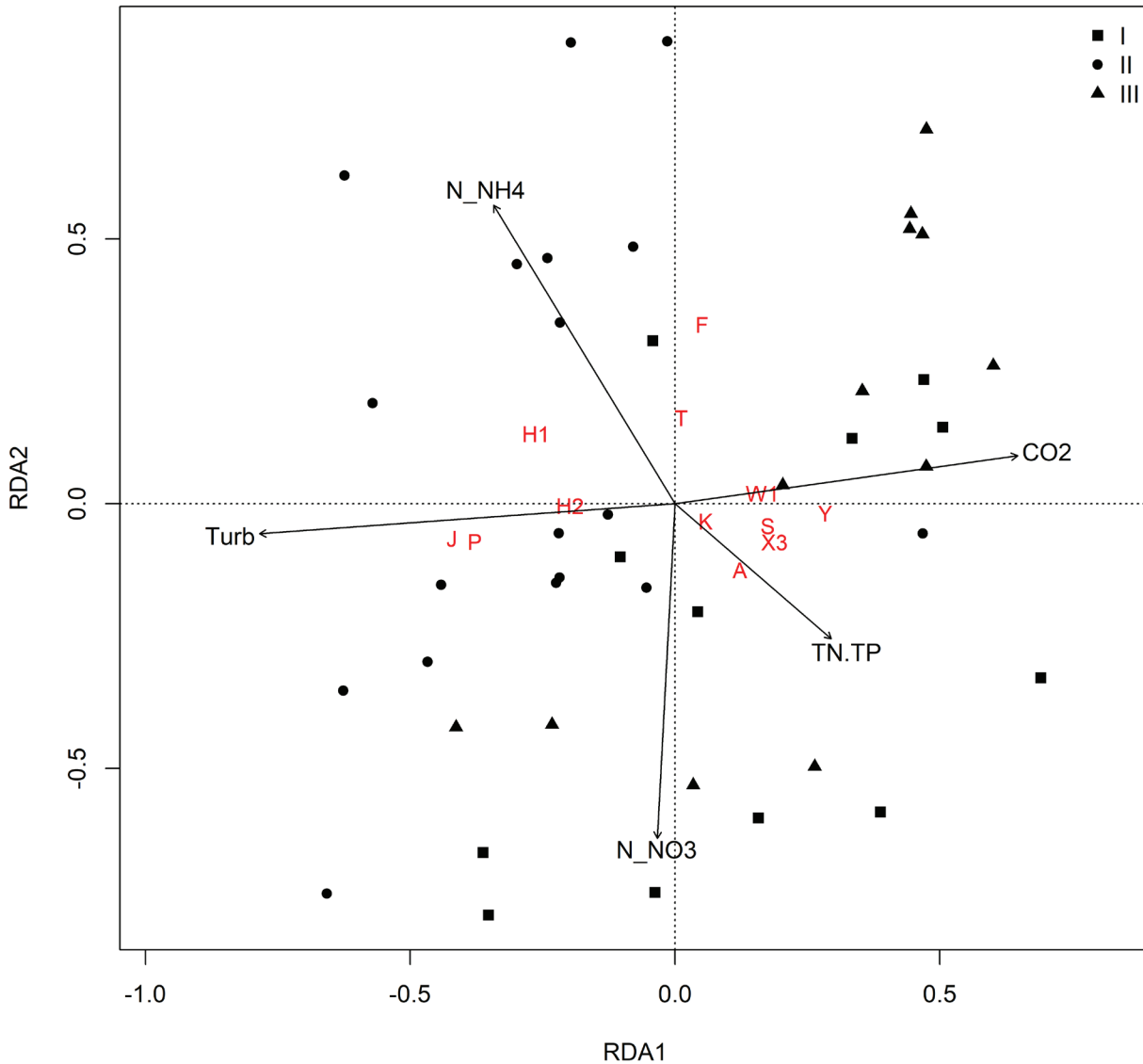
In this study, we sought to understand the dynamics of the phytoplankton community and the RFG during a hydrological cycle from their relationships with the alternative states in a Pantanal floodplain lake. We found that the flood pulse is the driving factor of the seasonal variation of biomass, composition and functional groups.

Coqueiro Lake has two the alternative states proposed by Scheffer *et al.* (1993), the turbid and clear states have already been documented by Loverde-Oliveira & Huszar (2010). During the phase

of the clear water, the increase in transparency, maximum depth and stabilization of the water level, determine the limnological conditions favorable to the colonization by *Egeria najas*, especially in the areas with stronger lotic influence. Flood periods and high waters have a direct influence on the variables related to the availability of light and nutrients. Concentrations of total phosphorus cannot be considered as limiting to phytoplankton growth, but total nitrogen and reactive silica can be seen as limiting elements, at least at certain times of the year and in certain areas of the lake.

The studied system was highly diverse (annual mean = 3.1 bits ind<sup>-1</sup>), with a high representativeness of chlorophyceans in number of taxa during the low waters, being comparable to other floodplain lakes (Tezanos-Pinto *et al.* 2015, Machado *et al.* 2016). In





**Figure 5.** Redundancy Analysis ordination diagram of the sampling sites from environmental variables and functional groups of the phytoplankton in Coqueiro Lake, municipality of Poconé, state of Mato Grosso, Brazil. RFG classification based on Reynolds *et al.* (2002) and Padisák *et al.* (2009). Turb = turbidity; CO<sub>2</sub> = Carbon dioxide; TN:TP = ratio nitrogen/ phosphorus; NNO<sub>3</sub> = nitrate; NNH<sub>4</sub> = ammonium.

the Coqueiro lake, the variability in phytoplankton composition and biomass was mainly related to seasonal changes in the water level, with greatest biomass and highest species richness at the low water period and lowest at the high water period, after establishing connectivity with the main river and raised water in the lake. The inverse relationship between phytoplanktonic biomass and water level elevation has been widely documented for floodplain lakes of the Paraná (Bortolini *et al.* 2014), Amazon (Lobo *et al.* 2018), Paraguay (Oliveira &

Calheiros 2000) and temperate regions (Kasten 2003, Schemel *et al.* 2004).

According to the variability driven by the flood pulse functional groups have been used to explain the selection of dominant populations in tropical floodplains (Devercelli 2006, Nabout *et al.* 2006, Loverde-Oliveira & Huszar 2007, Bovo-Scomparin & Train 2008). In the Coqueiro Lake, stood out the groups K, P, F, J, H<sub>1</sub>, H<sub>2</sub>, characteristic of enriched and generally turbulent environments, including mainly cyanobacteria, chlorophyceans and diatoms.

During the low water period, the physical and chemical conditions of water mediated by the hydrological variations characterized the Coqueiro Lake as a shallow environment, with continuous mixing of the water column, high turbidity mainly of inorganic origin and high availability of nutrients, especially phosphorus. These conditions were favorable to the diatom and zygnematomycean species of the functional group P (*Aulacoseira* spp., Aulacoseirales, Aulacoseiraceae and *Closterium porrectum*, Desmidiiales, Closteriaceae), microplankton species and, in the case of diatoms, organisms adapted to live in turbulent environments, often turbid (Reynolds 1988, Sommer 1988) and eutrophic (Reynolds *et al.* 2002, Padisak *et al.* 2009). This group is usually also dominant in lotic environments (Bovo-Scomparin & Train 2008, Zanco *et al.* 2017).

In addition to diatoms, cyanobacteria, and zygnematomyceans, chlorophyceans also stood out in the Coqueiro Lake during the low water period: functional group J (*Hariotina reticulata*, Sphaeropleales, Scenedesmaceae), of common occurrence in enriched shallow lakes with good mixing (Reynolds *et al.* 2002) and group F, also occurring in the flood, formed by colonial green algae with a broad mucilage sheath. Although it is considered to be characteristic of poorly enriched lakes with clear epilimnion (Reynolds *et al.* 2002, Huszar *et al.* 2003), the group F had higher contributions in relatively high turbidity periods and good nutrient supply. In other tropical (Costa 2005) and subtropical (Kruk *et al.* 2002) environments, different species of the group F have also been reported for similar conditions.

The functional group A, formed by diatoms (*Cyclotella* sp., Stephanodiscales, Stephanodiscaceae) common in shallow, clear, mixed lakes (Reynolds *et al.* 2002), was exclusive to the receding, a period still with strong lotic influence and with high availability of silica and NID. However, the functional group T, characteristic of deep and mixed environments (Reynolds *et al.* 2002), occurred in the lakes under conditions of good availability of light and reactive soluble phosphorus. It should be noted, especially in the littoral site, the contribution of zygnematomyceans (*Bambusina borreri*, Desmidiiales, Desmidiaceae and *Mougeotia* sp., Zygnematales, Zygnemataceae) and oedogoniophyceans (*Oedogonium* sp.,

Oedogoniales, Oedogoniaceae) of the group T<sub>D</sub>, all exclusive to the period of high waters and common to the periphyton and metaphyton, besides the unicellular desmids (*Closterium setaceum*, Desmidiiales, Closteriaceae and *Staurodesmus validus*, *Cosmarium* spp., Desmidiiales, Desmidiaceae).

The species had a similar spatial distribution in the lake, regardless of the water flow or collection depth. Importantly is the establishment of connectivity with the river, increasing the contribution of flagellated algae in the limnetic sites. These groups are favored in high water periods (Oliveira & Calheiros 2000, Alves 2011, Lobo *et al.* 2018), since nanoplankton flagellates due to their rapid growth are able to maintain their populations. The nanoplanktonic organisms of functional group X<sub>3</sub> (chrysophyceans, Chromulinales) considered as typical of oligotrophic lakes with mixed layers, together with W<sub>1</sub> (euglenoids) and Y (*Cryptomonas* spp., Cryptomonadales, Cryptomonadaceae) were favored by the river-lake connectivity and indicate the tolerance of these functional groups to water flows (Domitrovic 2003).

Although nitrogen is not the most frequently limiting nutrient in tropical and subtropical lakes and reservoirs (Huszar *et al.* 2006), the phytoplankton of some Brazilian Pantanal lakes (Loverde-Oliveira & Huszar 2007) may be limited by this nutrient. In fact, phytoplankton biomass was directly related to the concentrations of dissolved inorganic nitrogen, but not to the concentrations of total P or SRP. On the other hand, assuming the levels of limitation to the growth of phytoplankton in general, from the semi-saturation constants for population growth (K<sub>s</sub>) in relation to reactive soluble phosphorus, dissolved inorganic nitrogen (3-5 µg L<sup>-1</sup> and 70-120 µg L<sup>-1</sup>, respectively; Reynolds 1997) and to the growth of diatoms in particular in relation to soluble reactive silica (42 µg L<sup>-1</sup>; Sommer 1988), mean concentrations of reactive soluble phosphorus (mean = 45 µg L<sup>-1</sup>) cannot be considered as limiting the growth of phytoplankton. As for dissolved inorganic nitrogen (mean = 117 µg L<sup>-1</sup>), it is possible to consider that there is a limitation to phytoplankton development in the Coqueiro Lake, at least at certain times of the year and in certain areas of the lake.

Considering the Coqueiro Lake as a whole and taking into account nutrient concentrations in relation to the semi-saturation constants

( $K_m$ ), none of the analyzed nutrients can be considered as limiting the growth, for example, of cyanobacteria. However, nitrate concentrations, may have moderately limited the growth of diatoms and chlorophyceans and strongly influenced the selection of dinoflagellates. As for soluble reactive silica, it was not expected to be one of the nutrients limiting the growth of diatoms in Coqueiro Lake, since the values of silicates found in Pantanal water bodies (Silva & Figueiredo 1999).

The N:P ratio was generally below that value (mean = 7.0) and, in fact, the cyanobacteria were co-dominant in much of the study and even developing bloom, albeit in a relatively restricted period. The low N:P ratio, almost always lower than 16 (Redfield *et al.* 1963), also suggest that nitrogen can be considered with a strong potential to limit phytoplankton growth in Coqueiro Lake. Studies considering shallow lakes along a latitudinal gradient (5°–55°S) in South America detected no relationship between the occurrence of cyanobacteria and the N:P ratio (Kosten *et al.* 2009).

There are strong empirical evidences that variations in the input of N and P can cause changes in phytoplankton composition (Philippart *et al.* 2000), especially in the Si:N and Si:P ratios, as potentially limiting elements for diatom growth, since the contribution of nitrogen and phosphorus has increased considerably with human activities, but not the input of silica (Cloern 2001). In the Coqueiro Lake, the Si: NID (atomic) ratio of the dissolved fraction was lower than 1 in the low water, rising and high water and greater than 1 in the receding, indicating potential limitation to diatom growth, except in the receding. The Si:P (atomic) ratio of the dissolved fraction was lower than 16 throughout the study, also pointing to a potential limitation by Si throughout the study.

Thus, the flood pulse is the main factor driving the seasonal variation in biomass, composition and RFG of the phytoplankton, during one seasonal cycle, in the different alternate states of Coqueiro Lake. The phytoplankton community presented reduced temporal variability in composition, but a wide variability in biomass. The limitation to phytoplankton growth by nutrients is related to the forms of dissolved nitrogen and, to a lesser extent, to silica, defining functional groups typical of turbulent and enriched environments.

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**Supplementary Material 1.** Relative contribution of the descriptor species of the Reynolds functional groups dominating the phytoplankton at each sampling site (municipality of Poconé, state of Mato Grosso, Brazil), in the periods of receding (PI), low water and beginning of the rising (PII) and end of the rising, high water and second receding (PIII).