Response of aquatic macrophyte biomass to limnological changes under water level fluctuation in tropical reservoirs

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Abstract

We evaluated the response of the biomass of aquatic macrophytes under limnological changes after water level fluctuation (WLF) of two tropical reservoirs (R1 and R2), located in northeastern Brazil. Initially we tested the hypothesis that post-WLF limnological conditions and biomass of macrophytes increase or decrease, depending on the variable or species. We monitored a 4×50 m permanent plot, in four expeditions per period (pre- or post-WLF), assessing species biomass and 10 limnological variables. We utilized 0.25×0.25 m quadrats for biomass. Once the effect of WLF in limnological variables and species biomass was confirmed, we utilized Canonical Correspondence Analysis to understand the relationship between limnological variables and species biomass. The abundant and/or dominant species in pre-WLF of R1 (*Pistia stratiotes*, *Eichhornia crassipes* and *Salvinia auriculata*) and R2 (*Paspalidium geminatum* and *S. auriculata*) reduced their biomass post-WLF and were correlated with temperature, total phosphorous and nitrate. The reduced biomass of *P. stratiotes*, *E. crassipes* and *S. auriculata* in post-WLF widened resource availability, allowing coexistence of species. Therefore, we suggest that the change of limnological conditions in post-WLF in artificial lakes acts only as a moderator factor of the interspecific interaction (especially coexistence), without direct relation between these conditions and species biomass.

Keywords: aquatic plant, limnology, plant ecology.

Resposta da biomassa de macrófitas aquáticas às mudanças limnológicas consequentes da variação do nível da água em reservatórios tropicais

Resumo

Avaliamos a resposta da biomassa de macrófitas aquáticas às alterações ambientais após flutuação do nível de água (WLF) de dois reservatórios tropicais (R1 e R2), localizados no Nordeste do Brasil. Inicialmente, testamos a hipótese de que após uma WLF as condições limnológicas e a biomassa das macrófitas aumentam ou diminuem, dependendo da variável ou espécie. Por isso, monitoramos uma parcela permanente de 4×50 m, em quatro amostragens por período (pré ou pós-WLF), avaliando a biomassa de espécies e 10 variáveis limnológicas. Utilizamos quadrados de $0,25 \times 0,25$ m na amostragem da biomassa. Uma vez que o efeito do WLF em variáveis limnológicas e biomassa das espécies foi confirmado, utilizamos a Análise de Correspondência Canônica para compreender a relação das variáveis limnológicas com a biomassa de espécies. As espécies abundantes e/ou dominantes no pré-WLF de R1 (*Pistia stratiotes*, *Eichhornia crassipes* e *Salvinia auriculata*) e R2 (*Paspalidium geminatum* e *S. auriculata*) reduziram sua biomassa pós-WLF, correlacionando-se diretamente com temperatura, fósforo total e nitrato. A redução da biomassa de *P. stratiotes*, *E. crassipes* e *S. auriculata* em pós-WLF ampliou a disponibilidade de recursos, permitindo a coexistência de espécies. Portanto, sugerimos que a mudança das condições limnológicas no pós-WLF em lagos artificiais atua apenas como um fator moderador da interação interespecífica (em especial a coexistência), sem relação direta entre essas condições e a biomassa das espécies.

Palavras-chave: planta aquática, limnologia, ecologia vegetal.

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1. Introduction

The present understanding of the ecology of aquatic ecosystems does not yet allow to delineate structuring of macrophyte communities in environments periodically influenced by water level fluctuations (WLF), such as artificial lakes (Zohary and Ostrovsky, 2011; Cunha-Santino et al., 2016; Moura Júnior et al., 2016). The intensity and duration of a WLF exerts relevant influence on the limnological conditions and on the ecological processes structuring aquatic communities, including the macrophytes (Wetzel, 2001). In general, a WLF causes changes of water volume, temperature, turbidity, electrical conductivity, tranparency and/or nutrients (Esteves and Camargo, 1986; Neiff, 1996; Esteves, 2011).

The studies on the response of biomass of aquatic macrophytes under a WLF show divergent results regarding the species (Byun et al., 2017). Some reports point out that after a WLF of intermediate intensity a reduction of the biomass of aquatic macrophytes occurs, inasmuch as their physiological capacities are exceeded (Paillisson and Marion, 2006; Lacoul and Freedman, 2006; Zohary and Ostrovsky, 2011; Bottino et al., 2013). In contrast, other works evidenced increase for biomass of particular species of macrophytes after WLF in rivers or tropical lakes (Neiff, 1975; Neiff et al., 2001; Menezes et al., 1993; Bini, 1996; Pompêo et al., 2001). Furthermore, there is no consensus upon the predictors of biomass of the macrophyte species under a WLF. Most specialists on aquatic macrophytes believe that the specificities of the water abiotic conditions after WLF determine the capacity of plant biomass production (Lacoul and Freedman, 2006; Henry-Silva et al., 2008; Zohary and Ostrovsky, 2011; Bottino et al., 2013). Some biotic variables such as interespecific competition and coexistence are relevant factors in the structuring of communities (Van Gerven et al., 2015; Moura Júnior et al., 2016) or biomass of aquatic macrophytes (Camargo and Florentino, 2000; Byun et al., 2017) in environment under variation of WLF.

In this context, we proposed a study to investigate the response of the biomass of aquatic macrophyte species after a WLF of intermediate intensity that occurred in two tropical artificial lakes. Initially we evaluated the hypothesis that WLF distinctly influence the biomass of the species of aquatic macrophytes and the limnological conditions. Once the hypothesis was confirmed, we had the following objectives: i – to understand the relation between the limnological variables and the species biomass in pre- and post-WLF of the reservoirs; and ii – to evaluate the patterns of coexistence for species biomass in post-WLF of the reservoirs.

2. Material and Methods

2.1. Description of the study area and the WLF event

The reservoirs Tapacurá – R1 (08° 02'32.1" S, 35° 11'46.5" W) and Cursai – R2 (07° 52' 41.6" S, 35° 10' 30.9" W) are located in the hydrographic basin of the Capibaribe River, northeastern Brazil (Figure 1). The R1 had a maximum depth of 108 m with a surface area of 58 Km^2 and maximum volume of 155 million m^3, while R2 reached 95 m deep, area of 58 Km^2 and volume of 24 million m^3 (SRHE, 2015).
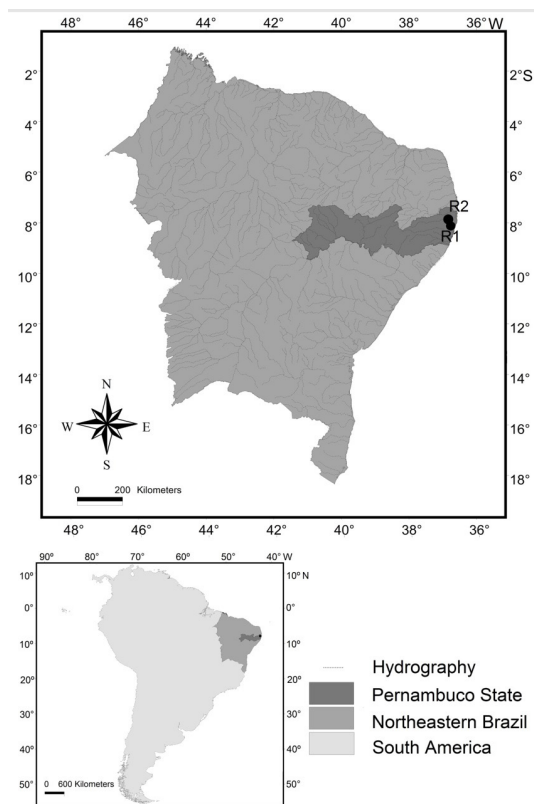

Figure 1. Map of Northeastern Brazil and the geographic location of the Tapacurá (R1) and Cursai (R2) Reservoirs.

The average monthly rainfall in the watershed of the reservoirs varies from 221 mm to less than 70 mm (APAC, 2016). In June 2010, the meteorological station of Tapacurá recorded 448 mm of rain, when 307 mm fell within only 10 days (APAC, 2016). Such heavy rains caused a WLF of up to 8 m in the Capibaribe river, being qualified by Moura Júnior et al. (2016) as an intermediate flood event.

2.2. Sampling period and data collection

We made eight sampling expeditions to each reservoir: four before water level fluctuation (pre-WLF) and four after (post-WLF). Field work in the pre-WLF period was done in November 2008, and May, August and December 2009, and the post-WLF in August and November 2010, and February and June 2011.

We established a 5 m × 40 m rectangular permanent plot in each lake. The shortest limits of the plot were perpendicular to the shore and the longest parallel to the shore. The aquatic macrophyte stand where we established the permanent plot of R1 and R2 had mean width of 5 m in all field expeditions. This way, the permanent plot covered all assemblages of aquatic plant types described by Cook (1996), except amphibious. The criteria to place the permanent plot were the same utilized by Moura Júnior et al. (2016).

At each sampling, the permanent plot was evaluated regarding species biomass and limnological variables. Sampling of the species biomass followed the sampling

quadrats technique according to Howard-Williams (1975). Within the permanent plot we placed 0.25×0.25 m quadrats where each species presented cover above 0.0625 m². We collected one to twelve sampling quadrats per species, depending on the number of their plant groups in the permanent plot. We prioritized sampling in banks of different distances from the shore, so we could capture variations of the species biomass proveniences from the depth gradient. The biomass collected in quadrats of a same species were added together, this sum being made for each sampling period.

The emergent or floating aquatic macrophytes were collected manually or with a 50 mm mesh net, and the submerged utilizing a 1 cm mesh immersion net or an iron stick with hooks. The plants collected in each quadrat were identified, kept in labeled plastic bags, and taken to the Laboratory of Floristics of Coastal Ecosystems (LAFLEC) of the Federal Rural University of Pernambuco (UFRPE). The biological material was washed to remove the sediment. We identified the collected material using taxonomic keys available in the literature and morphological comparison with exsiccate deposited in the herbarium Vasconcelos Sobrinho (PEUFR) at UFRPE.

Next, this plant material was put in paper bags and oven dried at 70 °C until constant weight and ash free. The dry biomass of each species was weighed on digital balance (± 0.001 g), the values being expressed in grams of dry mass per square meter (gDW/m²).

The limnological variables conductivity – Con ($\mu S. cm^{-1}$), dissolved oxygen – DO ($mg.L^{-1}$), pH, temperature – Tem (°C) and turbidity – Tur (NTU) were assessed in the field using a multiparameter probe (YSI, model 556 MPS - Multiprobe System), and transparency – Secchi (m) with the Secchi disc. The concentrations of nitrate - NO_3 ($mg.L^{-1}$), nitrite – NO_2 ($mg.L^{-1}$), phosphate – PO_4 ($mg.L^{-1}$) and total phosphorous – TP ($mg.L^{-1}$) were determined following laboratorial protocols (Golterman et al., 1978; Mackereth et al., 1978; Valderrama, 1981). The water samples for laboratorial analysis and the multiparameter readings were taken in duplicate from the sub-surface (0.25 cm deep) in the plot edges. The samples for laboratorial analyses were manually collected, kept in 500 mL bottles and cooled to avoid oxidizing the nitrogen and phosphate compounds and taken to the Limnology Laboratory of UFRPE.

2.3. Analyses of data

Species biomass was treated per sampling period (pre- or post-WLF) and the permanent plot was considered our sampling unit. We assembled two matrices of data: A - matrix of species biomass per expedition and sampling period; B - matrix of the limnological variables per expedition and sampling period. The first matrix included the data of biomass of species present in more than 10% of samples (Causton, 1988).

We transformed the data of the matrices A and B ($\log x + 1$) and applied the tests of Shapiro-Wilk and Cochran to evaluate if the data were normal and homoscedastic, respectively, what was confirmed. We elaborated new matrices A and B,

now with transformed data. We utilized Analysis of Variance (ANOVA) to evaluate differences in species biomass and limnological variables in pre- or post-WLF.

We applied a forward selection to indicate the explicative limnological variables (Blanchet et al., 2008) of the biomass of macrophytes recorded in the permanent plot of R1 and/or R2, optimizing the matrices A and B with transformed data. Next, we applied Canonical Correspondence Analysis (CCA) to examine the explanatory limnological variables correlated with species biomass. We applied a Monte Carlo permutation test (999 permutations) to verify the significance of the correlations indicated by the final CCA and the number of significant axes of this analysis. The ANOVAs, Shapiro-Wilk, Cochran, forward selection, and CCAs were performed using the software R (R Core, 2013). We utilized the packages "vegan" to compute ANOVA and CCA, beside "forward" to compute a forward selection.

3. Results

3.1. Evaluation of hypotheses

We detected significant differences of the variables Con, Tur, PO_4, TP, DO and NO_3 between the periods pre- and post-WLF of R1 and/or R2 (Table 1). We recorded distinct responses in the species biomass in post-WLF (Table 2).

3.2. Limnological variables and biomass of the species

The variables Tur and TP presented reduction in Post-WLF of R1 and R2. The concentration of PO_4 decreased in Post-WLF of R2, and DO increased in R1 for the same period. Con decreased in Post-WLF of R1 and increased for R2 in the same period (Table 1).

The species *Eichhornia crassipes* (Mart.) Solms was dominant regarding the total biomass recorded in different sampling periods of R1, and *Pistia stratiotes* L. and *Salvinia auriculata* Aubl. were abundant in pre-WLF. These species presented reduction in biomass in post-WLF, while *Polygonum ferrugineum* Wedd. increased its biomass in the same period. *Ceratopteris pteridoides* (Hook.) Hieron. was only recorded in pre-WLF, and *Hydrocotyle ranunculoides* L.f. and *Ludwigia helminthorrhiza* (Mart.) H. Hara in post-WLF of R1 (Table 2).

In R2, the species *Paspalidium geminatum* (Forssk.) Stapf and *S. auriculata* were abundant in the distinct sampling periods, while *L. helminthorrhiza* was abundant in post-WLF (Table 2). *Eichhornia crassipes*, *P. geminatum* and *S. auriculata* presented reduced biomasses in post-WRL of R2, while *L. helminthorrhiza* increased its biomass in the same period (Table 2). The species *P. ferrugineum* and *H. ranunculoides* were recorded exclusively in pre-WLF and *Oxycaryum cubense* (Poepp. & Kunth) Lye in post-WLF of R2 (Table 2).

3.3. Limnological variables × biomass

According to forward selection only DO, Tem, NO_3 and TP were correlated with the macrophytes biomass in R1 and R2. (Table 3). The Monte Carlo test indicated satisfactory performance of the CCA (p = 0.003) for both

Table 1. Means and standard deviations (SD) of the limnological variables assessed in the permanent plot for pre- or post-water level fluctuation (WLF) periods in the Tapacurá and Cursai Reservoirs. Results of ANOVA (t) between means of the limnological variables.

Variables (unit of measurement)	Cursai		Tapacurá	
	Pre-WLF	Post-WLF	Pre-WLF	Post-WLF
	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD
Conductivity ($\mu S. cm^{-1}$)	286 ± 28.08	310.25 ± 43.43**	458.50 ± 41.03	423.25 ± 17.63***
Dissolved oxygen ($mg.L^{-1}$)	5.55 ± 0.92	5.88 ± 0.45	4.05 ± 1.17	5.77 ± 1.74*
Nitrate ($mg.L^{-1}$)	1.07 ± 0.33	1.67 ± 0.18	1.05 ± 0.33	0.70 ± 0.23
Nitrite ($mg.L^{-1}$)	0.78 ± 0.32	0.26 ± 0.6	1.15 ± 0.40	2.20 ± 1
Orthophosphate ($mg.L^{-1}$)	2.14 ± 0.04	1.11 ± 0.08*	2.62 ± 0.22	2.30 ± 0.08
pH	7.42 ± 0.29	7.53 ± 0.53	7.20 ± 0.28	7.27 ± 0.38
Secchi (m)	0.55 ± 0.05	0.72 ± 0.09	0.40 ± 0.08	0.52 ± 0.05
Temperature (°C)	28.35 ± 2.25	28.17 ± 2.35	28.97 ± 0.86	28.35 ± 2.07
Total phosphorous ($mg.L^{-1}$)	2.31 ± 0.27	1.5 ± 0.17*	7.27 ± 0.05	2.55 ± 0.12***
Turbidity (NTU)	73.22 ± 23.49	43.5 ± 23.78**	57.67 ± 3.25	71.42 ± 4.67***

* $p < 0.05$; ** $p < 0.001$; *** $p < 0.0001$.

Table 2. Mean and standard deviation (SD) of the total biomass (DW/m^2) of the species recorded in the sampling units of the Cursai and Tapacurá reservoirs, during the pre- and post-Water Level Fluctuation (WLF) periods. Results of ANOVA (t) between means of the species biomass.

Species	CURSAI		TAPACURÁ	
	Pre-WLF	Post-WLF	Pre-WLF	Post-WLF
	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD
Pistia stratiotes L.	-	-	112.4 ± 9.14	26.4 ± 16.7**
Hydrocotyle ranunculoides L.f.	1.3 ± 2.7	-	-	4 ± 3.4
Oxycaryum cubense (Poepp. & Kunth) Lye	-	14.7 ± 10.0	-	-
Ludwigia helminthorrhiza (Mart.) H. Hara	4.3 ± 6.3	85.0 ± 8.5**	-	4.0 ± 8.0
Paspalidium geminatum (Forssk.) Stapf	249.5 ± 50.1	94.7 ± 50.1**	-	-
Polygonum ferrugineum Wedd.	12.7 ± 14.9	-	0.7 ± 0.3	4.3 ± 0.3**
Eichhornia crassipes (Mart.) Solms	19.7 ± 2.83	2.3 ± 2.7*	861.3 ± 63.8	410.7 ± 38.6**
Ceratopteris pteridoides (Hook.) Hieron.	-	-	1.7± 3.4	-
Salvinia auriculata Aubl.	127.0 ± 28.7	98 ± 54.1*	65.9 ± 28.9	31.3 ± 16.5*

- species not recorded in the samples; * $p < 0.001$; ** $p < 0.0001$.

Table 3. Forward selection results indicated correlation between abiotic variables and macrophyte biomass in R1 and R2.

Variable	*p* value	R^2
Total phosphorous	< 0.001	40.28
Dissolved oxygen	< 0.001	26.12
Nitrate	0.010	12.64
Temperature	0.021	2.16
Conductivity	0.059	0.21
Inorganic phosphate	0.072	0.18
Nitrite	0.091	0.11
Transparency	0.102	0
Turbidity	0.190	0
pH	0.211	0
Total	**< 0.001**	**81.70**

R^2: percentage of explained variance.

first axes (Figure 2). The axes 1 or 2 of the CCA expressed relations between the limnological variables selected by the preliminary CCA and the biomass of the abundant species in pre- and post-WLF of R2 (axis 1) or R1 (axis 2).

The CCA did not point clear relations between the biomass of *P. geminatum* and the limnological variables. In R1, the biomass assessed for *E. crassipes*, *P. stratiotes* and *S. auriculata* in the sampling units of pre-WLF presented direct correlation with NO_3 and Tem and inverse with DO. In contrast, the biomass recorded in post-WLF for *O. cubense* was inversely correlated with NO_3 and Tem and directly with DO (Figure 2). The biomass of *S. auriculata* in pre-WLF of R2 was directly correlated with Tem, TP and NO_3 and inversely with DO, while the biomass of *L. helminthorrhiza* and *O. cubense* in Post-WLF showed inverse relation with Tem, TP and NO_3 and direct with DO (Figura 2).
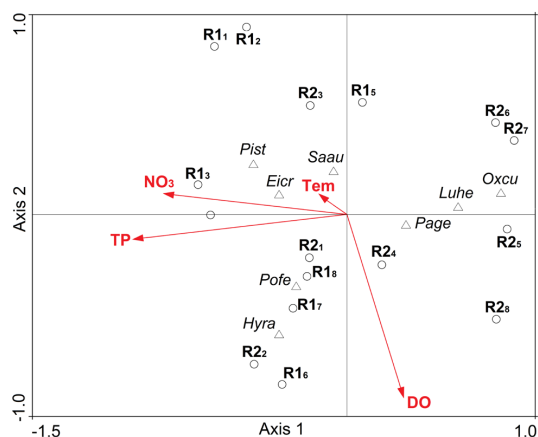
Figure 2. Representation of the Canonical Correspondence Analysis (CCA) according to the biomass of aquatic macrophytes in the sampling units of pre- and post- Water Level Fluctuation (WLF) in the Tapacurá (R1) and Cursaí (R2) Reservoirs. ($_{1,2,3,4}$) – number of sampling units of the R1 and R2 during the pre-WLF; ($_{5,6,7,8}$) – number of sampling units of the R1 and R2 during the post-WLF; (○) - sampling unit; (Δ) - macrophyte species; (Pist) - *Pistia stratiotes*; (Eicr) - *Eichhornia crassipes*; (Saau) - *Salvinia auriculata*; (Pofe) - *Polygonum ferrugineum*; (Hyra) - *Hydrocotyle ranunculoides*; (Page) - *Paspalidium geminatum*; (Luhe) - *Ludwigia helminthorrhiza*;(Oxcu)-*Oxycaryum cubense*;(Tem)-temperature; (NO$_3$) - nitrate; (TP) - total phosphorus; (DO) - dissolved oxygen.

4. Discussion

We confirmed the hypothesis that one WLF causes changes in the limnological conditions and species biomass of aquatic macrophytes. Biomass productivity of aquatic macrophytes is related with their capacity to absorb NO$_3$ and/or PO$_4$, transforming them in organic compounds (Camargo et al., 2003; Henry-Silva et al., 2008; Bottino et al., 2013). Species of the genera *Pistia*, *Salvinia* or *Eichhornia* present high stocks of N or P in their tissues (Martins et al., 2003; Henry-Silva and Camargo, 2000, 2006), moreover when submitted to an environment of reduced WLF (Neiff et al., 2008; Medeiros et al., 2016). Water temperature is also a variable directly related with the production of aquatic plant organic matter (Bottino et al., 2013). Such information explains the results of biomass of *E. crassipes*, *P. stratiotes* and *S. auriculata* in pre-WLF of R1 or R2, as well as the correlations between species/limnological variables obtained by CCA. We believe that the representatively of *P. geminatum* in the amount of biomass verified in both analyzed periods in R2 has masked its relation with the limnological variables evaluated in the CCA.

However, a WLF of intermediate or large intensity causes loss of structural compounds in aquatic macrophytes, favoring the appearance of debris which cause plant death (Pompêo and Moschini-Carlos, 2003). Aquatic macrophytes rapidly degrade labile or refractory fractions when influenced by WLF in reservoirs (Bianchini Júnior, 1997). Such mentioned inferences were corroborated by the reduction of biomass of *P. stratiotes*, *S. auriculata* and

E. crassipes in Post-WLF of R1 and/or R2, as well as the correlations between species/limnological variables pointed by the CCA.

The inverse relation of Tem, NO$_3$ and/or PO$_4$ with *O. cubense*, *L. helminthorrhiza* or *P. ferrugineum* in the CCA called our attention, once these species are adjusted to waters rich in nitrogenate and phosphate nutrients (Mormul et al., 2010; Meyer and Franceschinelli, 2011; Moura Júnior et al., 2011; Tsheboeng et al., 2014; Xavier et al., 2016). It is possible that the limnological variables indicated by the forward selection have indirect relation with the species biomass in Post-WLF. In this case, the limnological changes in post-WLF of R1 and R2 would act as moderators of other factors not evaluated in the CCA, that would have direct relation with the species biomass. We suggest that interspecific interactions (especially coexistence) is one of such factors. Hence, the limnological changes derived from WLF of R1 and R2 would widen the availability of resources for other species in post-WLF, allowing coexistence.

Such inferences are supported by the reduced biomass of *P. geminatum*, *P. stratiotes*, *S. auriculata* and *E. crassipes* in Post-WLF of R1 or R2, by the exclusive records of *O. cubense*, *L. helminthorrhiza* in Post-WLF and increased biomass of *P. ferrugineum* in R1 and *L. helminthorriza* in R2 in this last period. In a recent study, Moura Júnior et al. (2016) emphasized the direct influence of competition and coexistence between species in structuring the communities of aquatic macrophytes after the same WLF occurred in R2. They proved that the limnological changes derived from this WLF act as indirect factors of the structuring, and concluded that the limnological variables act only as moderator factors of the interspecific interactions in Post-WLF situations. Other works verified the extraordinary capacity of the interspecific interactions between macrophytes to influence the growth of biomass of these plants (Camargo and Florentino, 2000; Byun et al., 2017) or the low relation between physical-chemical variables of the water and structuring of aquatic macrophyte communities in tropical reservoirs (Cunha-Santino et al., 2016).

In synthesis, we observed that the reduction of water temperature and the increased dilution of compounds essential for photosynthesis in post-WLF of R1 and R2 are inversely correlated with the biomass of the weeds *P. stratiotes*, *S. auriculata* and *E. crassipes* in that period. The reduction in their competitive capacity after the limnological changes derived from WLF of R1 and R2 increased the availability of resources for other species, allowing their coexistence. Therefore, we suggest that the change of the limnological conditions in post-WLF in R1 and R2 is a moderator factor of the interspecific interactions, notably coexistence. Yet, further investigations are needed to pinpoint definitive patterns upon biomass of aquatic macrophytes and their environmental predictors in situations of post-WLF. Nonetheless, we believe that the novelty of our study can highlight it as a theoretical mark on ecology of aquatic macrophytes, particularly for environments influenced by WLF from intermediate intensity flood.

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