

Water level fluctuations in a tropical reservoir: the impact of sediment drying, aquatic macrophyte dieback, and oxygen availability on phosphorus mobilization

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Abstract Reservoirs in semi-arid areas are subject to water level fluctuations (WLF) that alter biogeochemical processes in the sediment. We hypothesized that wet–dry cycles may cause internal eutrophication in such systems when they affect densely vegetated shallow areas. To assess the impact of WLF on phosphorus (P) mobilization and benthic P cycling of iron-rich sediments, we tested the effects of (i) sediment drying and rewetting, (ii) the impact of organic matter availability in the form of dried Brazilian Waterweed (*Egeria densa*), and (iii) alternating redox conditions in the surface water. In principle, drying led to increased P release after rewetting both in plant-free and in plant-amended sediments. Highest P mobilization was recorded in plant amendments under oxygen-free conditions. After re-establishment of aerobic conditions, P concentrations in surface water decreased substantially owing to P retention by sediments. In desiccated and re-inundated sediments, P retention decreased by up to 30 % compared to constantly inundated sediments. We showed that WLF may trigger biochemical interactions conducive to anaerobic P release. Thereby, *E. densa* showed high P release and even P uptake that was redox-controlled and superimposed sedimentary P cycling. Macrophytes play an important role in the uptake of P from the water but may be also a significant source of P in wet–dry cycles. We estimated a potential for the abrupt release of soluble reactive phosphorus (SRP) by *E. densa* of 0.09–0.13 g SRP per m² after each wet–dry cycle. Released SRP may exceed critical P limits for eutrophication, provoking

usage restrictions. Our results have implications for management of reservoirs in semi-arid regions affected by WLF.

Keywords Water level change · *Egeria densa* · Nutrient cycling · Eutrophication · Water management · Semi-arid · Itaparica reservoir

Introduction

Man-made aquatic systems, such as reservoirs in particular, often undergo frequent changes in water level due to operational water level manipulations or seasonal water availability (Nilsson 2009). Drying and rewetting of littoral sediments due to water level fluctuations (WLF) strongly influence sediment diagenesis and the function of littoral zones (Uhlmann et al. 2011, Krolová et al. 2013) including P cycling (Baldwin and Mitchell 2000, de Vicente et al. 2010) and therefore phytoplankton development (Rangel et al. 2012). Worldwide, most reservoirs fulfill multiple purposes (e.g., hydroelectric power generation, irrigation, flood control, domestic and industrial water use, aquaculture), but particularly those in areas of water scarcity are crucial to provide a reliable distribution of quality fresh water. Eutrophication appears as a major threat to water quality for these systems (Bergkamp et al. 2000; Smith 2003; Cooke 2005; Gunkel and Sobral 2013). The significance of WLF for lake management has been recognized for over a decade (Coops et al. 2003; Wantzen et al. 2008; Zohary and Ostrovsky 2011). However, management plans often still lack a comprehensive understanding of the linkage between hydrological and biochemical cycles to address “water-human-ecosystem interactions” (Wagener et al. 2010) to provide freshwater services and water quality.

Systems with shallow margins are especially sensitive to WLF, and their role in these ecosystems is not yet fully

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understood (Coops et al. 2003; Wantzen et al. 2008). The extent and timing of P release from littoral sediments can be crucial for primary production and water quality (e.g., Søndergaard et al. 2003). Several studies have shown increased P release from sediments following wet–dry cycles owing to the alteration of physical, microbial, and chemical processes within lake and reservoir sediments or at their sediment–water interface (Qiu and McComb 1994; Baldwin 1996; Mitchell and Baldwin 1998; Baldwin and Mitchell 2000, Watts 2000a; Batzer and Sharitz 2006). Finally, WLF cause exposure and desiccation of submerged macrophytes that can strongly influence the recycling of nutrients and the energy flow in aquatic ecosystems in their succession and at senescence (Granéli and Solander 1988; Marion and Paillisson 2003; Shilla et al. 2006; Kleeberg 2013). The high complexity of interacting processes of the internal P cycle complicates general predictions of response across different systems (see Baldwin and Mitchell 2000 for review), and most studies focused on the short-term implications of a single factor. Exposed sediments often undergo physical changes in their matrix, and particularly clay-rich sediments develop cracks and fissures. While sediment drying can promote the formation of amorphous iron (Fe)-oxides and thus P binding, mineral aging and particle size shifts may trigger the opposite by decreasing the P adsorption capacity (De Groot and Van Wijck 1993; Mitchell and Baldwin 1998; Qiu and McComb 2002; Gilbert et al. 2014). Furthermore, the organic matter content of sediments can become crucial for nutrient cycling when reflooding of desiccated sediments generates a nutrient pulse into the surface water (Watts 2000b; Smith and Jacinthe 2013). Recently, it was concluded that WLF have the capability to promote sediments to act as P sinks and in short term also as P sources, depending mainly on the variety of environmental conditions (Tang et al. 2014; Dieter et al. 2015). While there has been evidence that hydrological changes have impacts on the internal loading of P from different sediment types with different drying histories in wetlands (Aldous et al. 2005; Zak and Gelbrecht 2007; Gilbert et al. 2014), river floodplains (Kerr et al. 2010; Schönbrunner et al. 2012), and also in reservoirs (Watts 2000a, b; Wilson and Baldwin 2008 and literature mentioned above), the complex coupling of effects caused by WLF in densely vegetated reservoir sediments are not well known. In this study, we used the sediments of a shallow bay in the Itaparica Reservoir, NE Brazil, to run a mesocosm experiment to analyze the impact of wet–dry cycles and the effects of (i) sediment drying and rewetting, (ii) the amendment of organic matter in the form of dried *Egeria densa* substrate, and (iii) the presence and absence of oxygen in the water on P cycling.

We hypothesize that WLF significantly alter the way in which *E. densa* interferes with supposedly Fe-controlled

benthic P cycling in Icó-Mandantes Bay, Itaparica Reservoir. Thereby, phytoplankton development might be accelerated and cause water quality degradation.

Material and methods

Study site

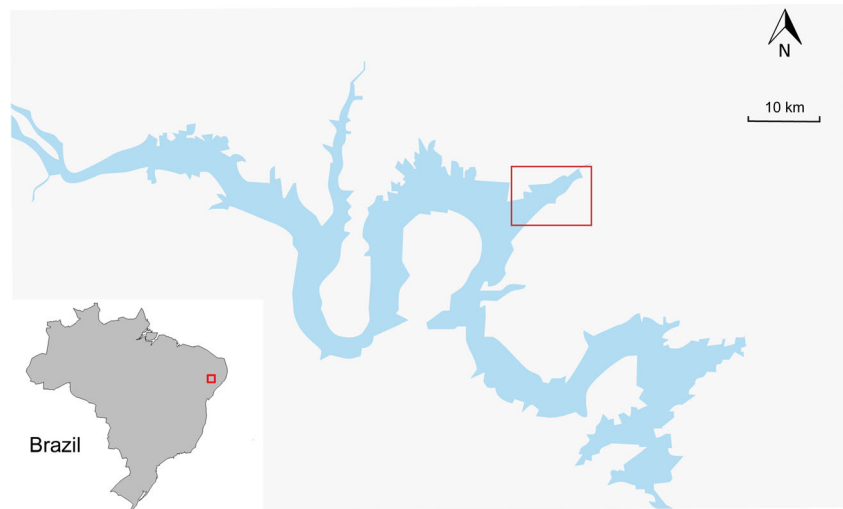
The study was conducted in Icó-Mandantes Bay (8° 49' 16.17" S, 38° 25' 30.86" W), one of the major bays in the Itaparica Reservoir in the São Francisco river, NE Brazil (Fig. 1). The Itaparica Reservoir has a regulated inflow of 2060 m³ s⁻¹, a length of 149 km, and a surface area of 828 km² (CHESF 2011). The maximum depth is 101 m, and the mean depth is 13 m. The rainy season extends from January to April with average annual precipitation of 420 mm. Average annual temperature is 26 °C. The Itaparica Reservoir has a particular significance in its semi-arid catchment area for drinking water abstraction, irrigation, hydropower generation, and other water exploitation purposes. In the past, the reservoir showed water quality issues with phytoplankton mass development and cyanobacteria (*Cylindrospermopsis raciborskii*) occurrence when minor P concentration elevations changed water quality significantly (Gunkel and Sobral 2013).

Periodic WLF of up to 5 m result from the imbalance of water availability and hydropower production due to seasonal variation of rainfall, high evaporation, and the almost constant generation of hydropower throughout the year (Gunkel et al. 2015). WLF in the reservoir can be significant and result in exposure and or desiccation of large sediment areas of several hundred square kilometers. Icó-Mandantes Bay has an area of 25 km², and almost half of the inundated area (~12 km²) can become dry under maximum WLF (aerial photograph analysis). We observed fluctuations exceeding 3.5 m during field campaigns in 2012–2013. The Brazilian Waterweed *E. densa* (henceforth termed *Egeria*) is the dominant submersed macrophyte species in the reservoir and occurs in large stands of high biomass (380–510 g per m²) in areas above 6–7 m water depth. These areas are affected by WLF and subjected to drying. Morphometric and chemical characteristics of the study site are given in Tables 1 and 2.

Field sampling

Sediment samples that were not yet affected by wet–dry cycles were collected from 7 m depth in October 2013 using an Ekman grab (Fig. 1; Table 2). We used unaffected sediment to capture the initial effect of WLF on sedimentary P cycling. Sediment samples were sieved (2 mm mesh size) to remove organic debris and snail shells and thoroughly mixed prior to experimentation. Macrophytes (*Egeria*) were harvested using

Fig. 1 Itaparica Reservoir and Icó-Mandantes Bay (rectangle in the right figure) in the São Francisco River, Brazil



a sampling rake and assorted for undamaged specimens. *Egeria* specimens were washed with reservoir water, the water was carefully shaken off, and plants were chopped and air dried until fully dehydrated.

Mesocosm experiment

A mesocosm experiment was conducted to study the effect of wet–dry cycles and decomposing *Egeria* on the mobilization of soluble reactive P (SRP), dissolved organic carbon (DOC), and the pore water concentrations of SRP and dissolved iron (DFe). Aliquots of the sediment slurry were used to fill 12 acrylic tubes ($h = 300$ mm; $d = 30$ mm), and water of the ionic strength corresponding to the reservoir ($80 \mu\text{S cm}^{-1}$ sodium chloride solution) was used to fill up the mesocosms. The water–sediment volume ratio was 3 to 1. Sediments were incubated at a temperature similar to the average reservoir water temperature (2012–2014: 27 ± 1 °C). All mesocosms were

closed and set aside for 2 weeks to compensate for possible disturbances before the start of experimentation. We used nylon litterbags (6×4 cm) with mesh openings of approximately $250 \mu\text{m}$ containing ~ 1 g of dried *Egeria*. *Egeria* litterbags were put on the sediment surface. The amount of added *Egeria* corresponded to the lowest biomass ranging of 380 g dry weight (dw) per m^2 determined for the vegetated sites of Icó-Mandantes Bay in 2013 (maximum observed biomass was 510 g dw m^{-2} after additional field surveys in 2014; Lima pers. comm.).

We used two sediment groups in our experiment: constantly wet sediment (“wet”) and sediment that had been dried and rewetted (“dry”). The latter was dried for 14 days until we recorded 25 % of gravimetric moisture loss and then rewetted. From the wet group, three replicates were amended with *Egeria* and named “wet-plant” while three un-amended replicates served as controls. In the same manner, three replicates from the dry group were amended with *Egeria* and named “dry-plant” while three replicates served as controls. In total, we used 12 mesocosms containing sediment. Another three replicates were set up with experimental water and *Egeria* but

Table 1 Basin morphometry and chemical characteristics of the surface water in Icó-Mandantes Bay in 2012 and 2013

Parameter	Unit	
Water level	m a.s.l.	299–304.5
Desiccation area	km^2	10–12
Volume	10^6 m^3	140
Water residence time ^a	Day	183 (68 in mainstream)
Soluble reactive phosphorus (SRP)	$\mu\text{g L}^{-1}$	3–6
Total phosphorus (TP)	$\mu\text{g L}^{-1}$	9–21
Total nitrogen (TN) ^a	mg L^{-1}	0.2–0.9
pH ^a	–	7.2–9.6
Conductivity ^a	$\mu\text{S m}^{-1}$	66–87

Water parameters were determined by standard analyses as described in Zwimmann et al. (1999)

^aData from Selge et al.(2015)

Table 2 Composition of sediment and *Egeria* (*Egeria densa*) from Icó-Mandantes Bay

Parameter	Unit	Sediment	<i>Egeria densa</i>
Organic matter (LOI)	% dw	8.5	86.0
Total carbon	% dw	2.8	35.7
Total nitrogen	% dw	0.3	2.0
Total phosphorus	mg g^{-1} dw	0.75	12.8
Iron (Fe)	mg g^{-1} dw	59.4	26.2
Fe/P	Molar	41.2	1.1

Sediment and plant parameters were determined by standard analyses as described in Zwimmann et al. (1999)

dw dry weight, LOI loss on ignition

no sediment (“only-plant”) to quantify P mobilization from *Egeria* without any influence of the sediment matrix. Accordingly, all treatments were done in triplicates; 15 mesocosms in five parallel treatments were set up for the whole experiment. By comparing “only-plant” to “wet-plant” and “dry-plant,” we could determine whether the sediment influences SRP mobilization (e.g., by P retention) and furthermore if that influence changes with drying.

The study site is characterized by atelomixis, i.e., day-night stratification changes (Gunkel et al. 2015). Calm or windless periods can prolong the stratification time and cause rapid oxygen depletion in the water column of Icó-Mandantes Bay (Keitel, unpublished data) and shallow tropical lakes in general (Townsend 1999). To adjust anoxic conditions, sediment mesocosms were sealed and oxygen concentrations in the mesocosms decreased quickly. We defined oxygen concentrations between 0.01 and 1.0 mg L⁻¹ as anaerobic conditions. Aerobic conditions were maintained by justifying oxygen concentrations between 6.0 and 8.0 mg L⁻¹ by aeration of the water column using aeration stones. In this way, we were able to alter redox conditions and realize water column mixing. To suppress the formation of thermal and chemical gradients in the water column, we used a magnetic float ball (a metal pin in a closed polypropylene container) to carefully stir the water from outside the closed mesocosms. Successively, five alternating redox phases were assessed over the course of the experimentation: phase 0 (start) = aerobic, phase 1 = anaerobic, phase 2 = aerobic, phase 3 = anaerobic, and phase 4 = aerobic. Oxygen measurements in the water were done by needle-type optical oxygen microsensors (Presens, Regensburg, Germany) injected through injection ports, allowing measurements in closed mesocosms.

All mesocosms containing sediment were equipped with a Rhizone pore water sampler (Rhizosphere Research Products, Wageningen, Netherlands) at 1 cm below the sediment–water interface, and pore water was collected via injection ports with a syringe. After reflooding of the mesocosms, samples were taken in intervals over a 70-day course.

Sample analyses

Surface water samples were analyzed for SRP and DOC concentrations. SRP was determined photometrically based on the molybdenum blue method (Murphy and Riley 1962) using a segmented flow analyzer (SFA, Skalar San^{plus}, Skalar Analytical B.V., De Breda). DOC concentrations were analyzed with a TOC/TN analyzer (multi N/C 3100, Jena Analytics, Jena, Germany). Because of the small sample volume (<2 mL), pore water was photometrically analyzed for SRP and DFe using a miniaturized procedure (Laskov et al. 2007). After sampling the overlying water, the volume removed was replaced with experimental water and dilution was considered in concentration calculations.

Aliquots of fresh sediments were used to determine dw (105 °C, 8 h) and organic matter content by loss on ignition (450 °C, 3 h) of dried sediments. Sediments were analyzed for TP after digestion of 5–10 mg dry sediment in 2 ml 5 mol l⁻¹ H₂SO₄, 2 ml 30 % H₂O₂, and 20 ml distilled water at 150 °C for 16 h (Zwirmann et al. 1999). Sediment concentrations of Fe were determined by atomic emission spectrometry (iCAB 7000 Series, Thermo Scientific) after wet digestion (HCl 37 %, HNO₃ 65 %, volumetric ratio 1:3) in a high pressure microwave oven (Gigatherm). C-N analyses were performed using dry sediment in a vario EL system (Elementar Analysensysteme GmbH, Hanau, Germany). All further *Egeria* analyses were done in accordance with sediment analyses. The P binding forms were determined by the sequential chemical extraction scheme of Psenner et al. (1984) with slight modifications (Hupfer et al. 1995). Briefly, six P species were separated in a sequential extraction manner: (1) pore water P and P loosely sorbed to surfaces (“NH₄Cl-P”); (2) reductant-soluble P, mainly Fe-hydroxide bound P (“BD-TP”); (3) P bound to Al- and Fe- oxides (“NaOH-SRP”); (4) P that has its origin in organic compounds (poly-P, P in humic substances) (“organically bound P;” “NaOH-NRP”); (5) acid-soluble P, mainly carbonate-P and apatite-P (“HCl-P”); and (6) residual P, determined after wet digestion of remaining sediment with sodium persulfate (Na₂S₂O₈) (“Res.-P”). Chemical analyses were always done as duplicates, and the average was used for data analyses.

Microbial biomass P was estimated by the fumigation–extraction method using ethanol-free chloroform to fumigate sediment samples, largely as described by Brookes et al. (1982). After fumigation with ethanol-free chloroform, P was extracted with NaHCO₃ solution. P from non-microbial organic matter is not released by chloroform fumigation (Brookes et al. 1982). Microbial P was determined by the difference of P from fumigated and non-fumigated sediment. We used 3–4 g fresh sediment (~1 g dw) rather than 10 g dw equivalent as suggested by the authors.

Statistical analyses

All statistical analyses were performed using R 3.0.2 (R Core Team 2013). We used linear mixed effects models from the “lme4” package (Bates et al. 2014) and two-way ANOVA. We tested the relationship between SRP and DOC mobilization in the surface water, and SRP and DFe mobilization in the pore water and three explanatory variables. The fixed variables were the following: (1) Treatment (two levels: *Egeria* and no *Egeria*), (2) Scenario (two levels: dry and wet), and (3) Redox (two levels: aerobic and anaerobic). After visual inspection of residual plots, response variables were log₁₀ transformed to reduce the spread of the data and to achieve assumption of normality (Crawley 2007). To account for the natural interaction between the variables, interaction terms were included for

all explanatory variables. Finally, we included random effects of time and mesocosm (i.e., experimental unit) as well as by-time and by-mesocosm random slopes for the response effect to account for any heterogeneity and temporal or spatial autocorrelation of replicate data collected from the same mesocosms (Zuur et al. 2009). To select significant explanatory variables, model selection was performed by stepwise backward model selection for each response variable discarding all variables with $P > 0.05$ from the final model (Crawley 2007). Comparisons between P extraction of fumigated and non-fumigated sediment of different sediment treatments were done with two-way ANOVA.

Results

Effect of sediment drying and rewetting, plant amendment, and oxygen availability on SRP mobilization

SRP release to the surface water increased significantly after sediment drying and rewetting, when *Egeria* was added and when redox conditions were anaerobic (full model including main and interaction effects of all three fixed variables: $\chi^2_{1 \text{ df}} = 4.6$, $P < 0.03166$, Fig. 2a). Each single effect (“Treatment,” “Scenario,” and “Redox”) affected SRP release significantly; the model comparison supported the full model as the best model and revealed the importance of interactions of the effects. Referring to our study system, this means that the interaction or the concurrent appearance of (i) dry sediments, (ii) *Egeria* material, and (iii) reducing conditions in the water promote a scenario that is most conducive for the release of SRP to the surface water (Fig. 2a). Redox conditions changed from aerobic to anaerobic within 1 day in the mesocosms. Both sediment-*Egeria* treatments showed strong reactions when redox conditions changed: surface water SRP concentrations increased significantly under anaerobic conditions and declined significantly when aerobic conditions were reestablished (Fig. 3). The uptake or release of SRP can be derived from Figs. 2a and 3; high SRP concentrations were mostly found under anaerobic conditions, indicating SRP mobilization from *Egeria*/sediment to the water and vice versa under aerobic conditions. The maximum SRP release was observed in the second anaerobic phase (phase 3) and was on average around 10 times higher than anaerobic phase 1. Alternating oxygen concentrations had a strong effect on SRP mobility (Fig. 3). However, the effect was only clearly recognizable in the *Egeria* treatments where additional plant P was present. Among all incubations, SRP concentrations were highest in “only-plant” mesocosms (Fig. 3). SRP mobility in “only-plant” mesocosms showed the same sensitivity towards water oxygen concentrations over the sequence of redox phases as observed in the treatments containing *Egeria* and sediment.

Effect of sediment drying and rewetting, plant amendment, and oxygen availability on DOC mobilization

Drying of sediments did not result in altered sedimentary DOC release compared with constantly wet sediments, irrespective of whether *Egeria* was added or not (Fig. 2b).

DOC release was high in all treatments containing *Egeria*; the addition of *Egeria* material affected the release of DOC significantly when compared with the controls without *Egeria* ($\chi^2_{1 \text{ df}} = 22.9$, $P < 0.001$; Fig. 2b). Furthermore, anoxic conditions caused an increase in DOC release to the surface water ($\chi^2_{1 \text{ df}} = 31.2$, $P < 0.001$, Fig. 2b) and the release of DOC was up to 10 times higher. DOC release in treatments without *Egeria* responded less strongly to changing oxygen concentrations.

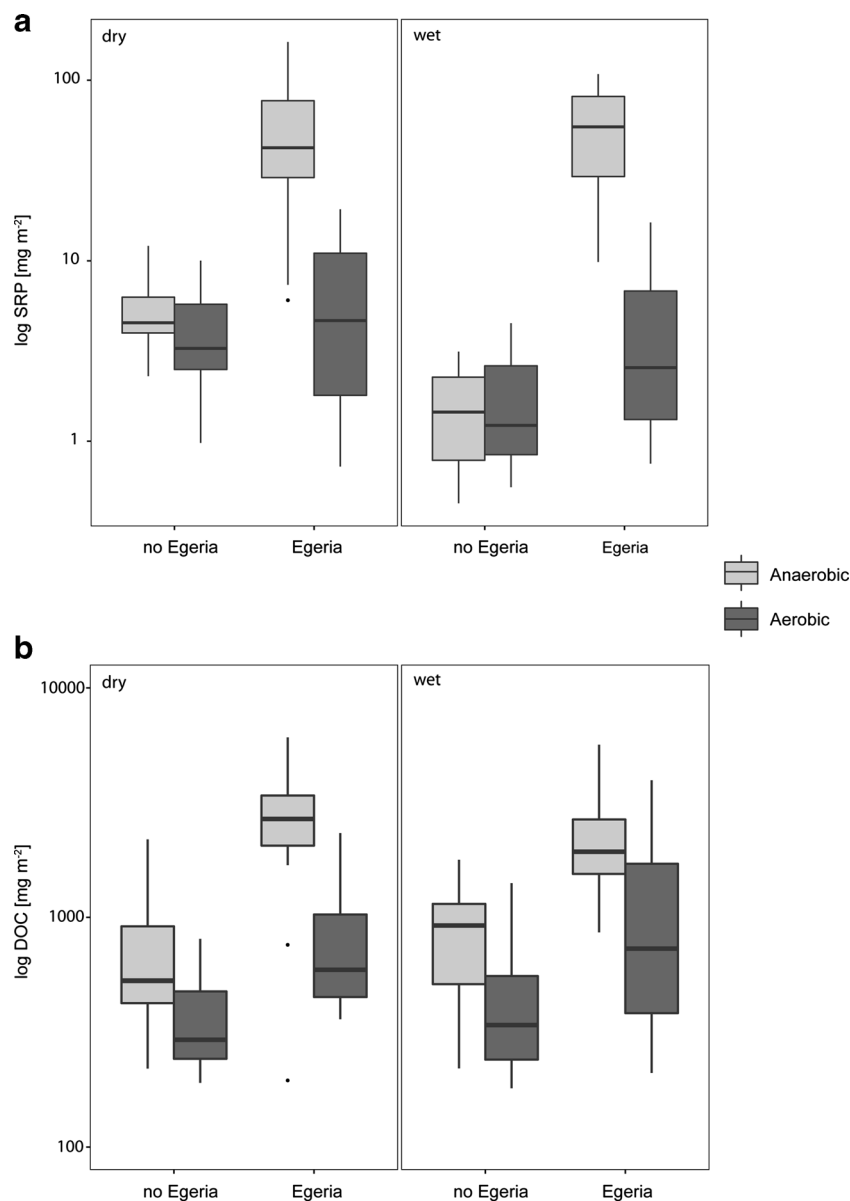
Effect of sediment drying and rewetting, plant amendment, and oxygen availability on pore water SRP and DFe

SRP and DFe concentrations were significantly affected by *Egeria* treatment (SRP: $\chi^2_{1 \text{ df}} = 20.6$, $P < 0.001$; DFe: $\chi^2_{1 \text{ df}} = 15.1$, $P < 0.001$, Fig. 4a, b). In all *Egeria* treatments, SRP and DFe pore water concentrations increased rapidly, while concentrations of the controls (“wet” and “dry” sediment without *Egeria*) remained constant. Highest SRP concentrations were between 1.0 and 1.3 mg L⁻¹ in “wet-plant” replicates and 0.4 to 1.0 mg L⁻¹ in “dry-plant” replicates. For “wet-plant,” DFe concentration reached its highest values from 23.2 to 47.9 mg L⁻¹ while values ranged between 13.2 and 157 mg L⁻¹ for “dry-plant” treatments. At the same time, the pore water SRP of *Egeria*-free controls remained relatively constant between 0.05 and 0.25 mg L⁻¹ (“wet”) and between 0.3 and 0.7 mg L⁻¹ (“dry”). DFe controls varied from 0.1 to 2.1 mg L⁻¹ (“wet”) and from 1.3 to 1.9 mg L⁻¹ (“dry”). Pore water SRP and DFe concentrations showed no clear correlation and were not significantly affected by the presence or absence of oxygen in the overlying water (Fig. 4a, b).

Phosphorus fractions and microbial P uptake

Sediment drying led to changes in Fe-associated P fractions (BD-P and NaOH-SRP), P that is bound to organic and bacterial biomass (NaOH-NRP), and also to mainly carbonate-associated HCl-P (Fig. 5). Fe-associated P fractions were dominant and varied between 42 and 46 % of total extractable P (P_{Te}) in the constantly wet groups and increased after drying to between 57 and 62 % of P_{Te} in the rewetted groups, regardless whether *Egeria* was added or not. Organically bound P, and P associated with bacterial biomass (NaOH-NRP), changed noticeably after drying and varied between 27 and 33 % in “wet” and 15 and 18 % (“dry”) relative to P_{Te} . Dried and rewetted sediments showed the tendency to consist of

Fig. 2 Boxplots showing the effects of sediment drying, *Egeria* addition, and oxygen concentration on **a** soluble reactive phosphorus (*SRP*) release and **b** dissolved organic carbon (*DOC*) release into the surface water. The *line* in the middle of the box represents the median, the lower and upper ends of the box are the 25 and 75 % quartiles, respectively. *Light grey* boxes denote anaerobic conditions in the surface water, *dark grey* boxes denote aerobic conditions. *dry* dry sediment, *wet* wet sediment, *Egeria* *Egeria* addition, *no Egeria* no *Egeria* addition



more redox-sensitive P but of less organically bound P compared with constantly wet sediments.

Potentially mobile P (P_{mob}) was defined as the sum of loosely adsorbed P ($\text{NH}_4\text{Cl-P}$), redox-sensitive P (BD-TP), and organically bound P (NaOH-NRP). HCl-extractable P clearly decreased in “dry” groups (9–11 %) compared with “wet” groups (15–17 %). Residual P ranged between 9 and 10 % (“wet” groups) and 13 and 15 % (“dry” groups). However, drying effected P extraction and P recovery was low (~70 %).

The addition of *Egeria* did not seem to affect the amount and composition of P binding forms in both “wet” and “dry” sediments (Fig. 5).

P extraction was significantly higher after chloroform fumigation compared to unfumigated sediment ($F(1, 16) = 15.53$,

$P = 0.0012$) (Fig. 6). Both plant-amended treatments showed significantly increased extractable P when compared to wet sediment without *Egeria* addition ($F(3, 16) = 8.489$, $P = 0.0013$).

Discussion

Water reservoirs are often affected by severe water level changes, which can influence different processes decisive for internal P mobilization. By simulating WLF to study the interaction of such processes, we tried to prove the hypothesis that WLF possess the ability to contribute to internal eutrophication.

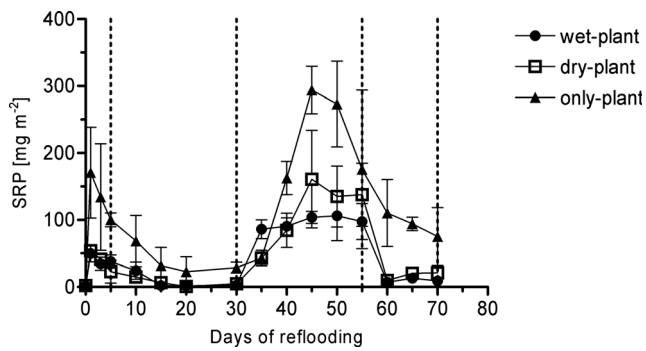
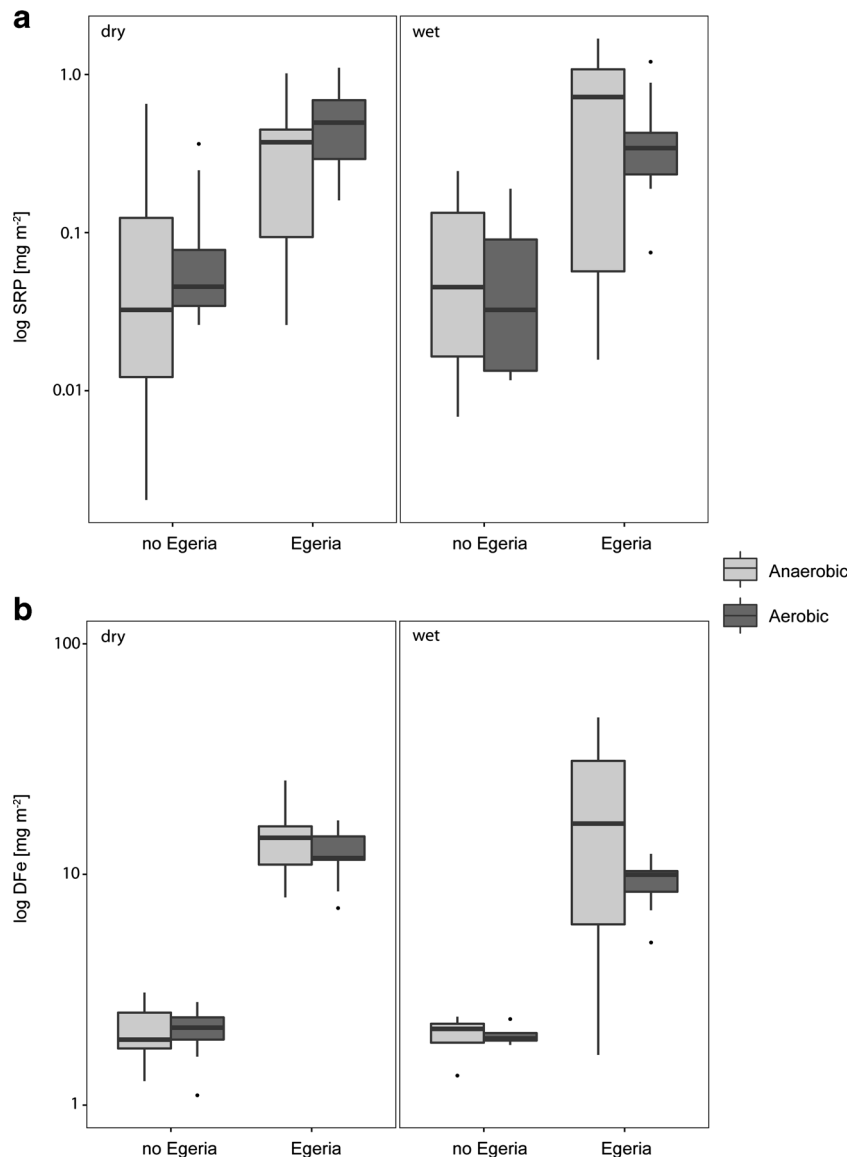


Fig. 3 Variation of soluble reactive phosphorus (SRP) in plant-amended sediment and plants without sediment under four alternating redox phases (indicated by the dotted lines 1–4). The experiment started aerobic and turned anaerobic during 1 day of reflooding. *Wet-plant* constantly wet sediment with *Egeria*, *dry-plant* rewetted sediment with *Egeria*, *only-plant* *Egeria* in water without sediment. Symbols represent averages with error bars showing one standard deviation

WLF can cause drying and rewetting of sediments and thereby promote the spontaneous release of P to the water column that can be more pronounced in comparison to constantly wet sediments (De Groot and Van Wijck 1993; Qiu and McComb 1995; Watts 2000a; Gilbert et al. 2014; Tang et al. 2014). Our results agreed with those previous findings in showing an increased SRP release from rewetted sediments, likely generated by bacterial P release after cell lysis of bacteria (Gordon et al. 2008) or after aerobic mineralization of organic matter and the resulting release of P (Watts 2000b, Smith and Jacinthe 2013). The reduced yield of HCl-extractable P in “dry” groups compared with the “wet” groups indicated an increased dissolution and loss of Ca–P bindings after drying of sediments. Smith and Jacinthe (2013) observed a shift towards more soluble calcium-phosphate minerals due to drying. In our work, drying caused compaction of the

Fig. 4 Boxplots showing the effects of sediment drying, *Egeria* addition, and oxygen concentration on concentrations of **a** SRP and **b** dissolved iron (DFe) in the pore water. The line in the middle of the box represents the median, the lower and upper ends of the box are the 25 and 75 % quartiles, respectively. Light grey boxes denote anaerobic conditions in the surface water; dark grey boxes denote aerobic conditions. *dry* dry sediment, *wet* wet sediment, *Egeria* *Egeria* addition, *no Egeria* no *Egeria* addition



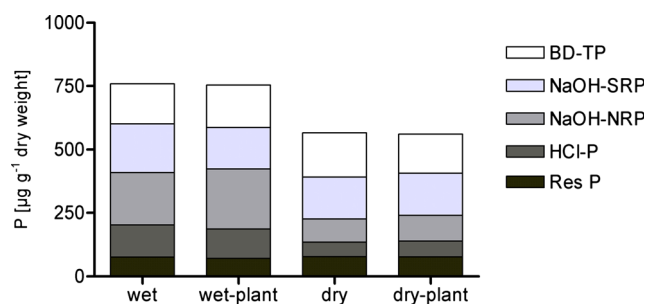


Fig. 5 Composition of phosphorus (P) fractions determined by sequential extraction of sediment that was constantly wet (*wet*), dried and rewetted (*dry*), and additionally amended with *Egeria* (*wet-plant*, *dry-plant*). Loosely adsorbed P ($\text{NH}_4\text{-Cl}$ fraction) accounted for less than 1 % and is not shown. Data are means of laboratory duplicates of surface sediment (0–1 cm)

sediment that might be one reason for the lowered P recovery by extraction compared with non-dried sediments. The sum of P fractions was notably less than the direct P measurement in the “dry” group; i.e., the P recovery was low (~70 %). Accordingly, the interpretation of fractionation results for dried sediments should be handled with caution. Therefore, it is not clear if plant amendment and subsequent redox changes significantly affected the P -binding forms of the sediment substantially. The studied sediment is characterized by a high Fe/P ratio (>40; molar) indicating a high binding capacity at the surface of Fe -hydroxides. Despite the strong redox dependency of P bound to Fe -hydroxides (Jensen et al. 1992), the high Fe inventory may constitute P uptake, even under anaerobic conditions, as long as not all Fe is in its reduced form or the sediments are not yet P saturated.

Pore water SRP and DFe concentrations increased after plant amendment but showed unambiguous reactions to changes in oxygen concentration in the overlying water. Although the redox conditions did not affect the mobility of DFe according to our statistical analysis, we observed a time shift between fluctuating DFe concentrations and alternating oxygen concentration; that is, the highest DFe concentrations occurred shortly after oxygen concentrations reached the

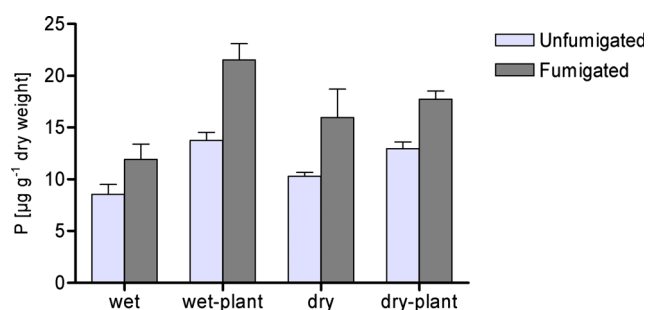


Fig. 6 Sediment extractable phosphorus (P) in unfumigated (control) and fumigated samples. *wet* constantly wet sediment, *dry* rewetted sediment, *wet-plant* constantly wet sediment with *Egeria*, *dry-plant* rewetted sediment with *Egeria*

minimum (data not shown). Diffusive oxygen transport in sediments is time-dependent and can cause a delayed reaction to oxygen concentrations in the overlying water (Precht and Huettel 2004). Pore water DFe was either enriched by *Egeria*-derived Fe or the addition of *Egeria* caused an increased dissolution of sediment Fe . However, increased concentrations of pore water SRP and DFe did not concur with an increase of those concentrations in the surface water (surface water DFe data not shown). Neither the composition of P fractions nor pore water analyses proved a clearly Fe -controlled benthic P cycling in the reservoir.

There is some evidence that the macrophyte substrate was mainly controlling the release/uptake of P . The P -dynamic we observed in “only-plant” treatments showed a strong redox-sensitive P mobility and therefore support the assumption of an *Egeria*-dominated P cycle under given conditions. Compared to the sediment, the added *Egeria* material was very rich in P (Table 2) and varying amounts of that added P were recovered in the different treatments as SRP to the overlying water. Within the different treatments, observed water SRP concentrations were in rank order “only-plant” > “dry-plant” > “wet-plant.” The order corresponded to a recovery of added plant P of $10 > 6 > 4$ % in the overlying water. This means the presence of “wet” and “dry” sediment was able to retain ~40 % (in “dry-plant”) and ~60 % (in “wet-plant”) of the mobilized plant P , respectively, even under anaerobic conditions (see oxygen-dependent SRP availability in Fig. 4). This finding indicates that the sediment lost more than 30 % of its capacity to retain P after drying. But, more importantly, it showed that the release and uptake of P is mainly controlled by *Egeria* as the main driver of P mobilization and that the sediment plays a less important role. However, it should be noted that *Egeria* amendment may lower the redox conditions in the sediment so that P bound to redox-sensitive compounds might be released or the P binding capacity and affinity of sediments might be lowered, respectively.

Surprisingly, we found the same oxygen-controlled P mobilization pattern in all *Egeria* treatments regardless of whether sediment was present or not. *Egeria* from Itaparica is characterized by a high Fe content (Table 2) that might interfere with a redox-sensitive Fe – P coupling at the water–plant interface, but the analyses of mesocosm surface water did not reveal a correlation of SRP and DFe (data not shown). On the other hand, microbes are known to induce P release via hydrolyses of poly- P under anoxic conditions (see Hupfer et al. 2007 for review). The fact that bacteria can store excess P as poly- P during aerobic conditions and hydrolyze poly- P during subsequent anaerobic conditions may further explain the redox-driven release and uptake of P in our *Egeria* treatments. It was found recently that plant litter can indeed accumulate P and that microbial activity is likely to trigger the process (Cheesman et al. 2010). In our work, microbial biomass P indicated that *Egeria* addition stimulated microbial P

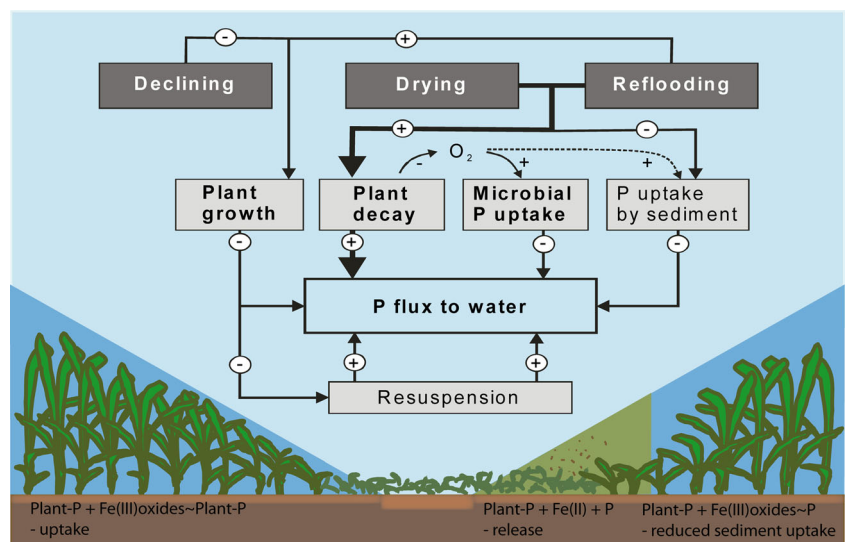
turnover. *Egeria* substrate certainly carried microbes that were then introduced to the mesocosms while at the same time *Egeria* was an extra C-source that could further fuel microbial activity in the sediment. Therefore, the role of microbial biomass in P cycling can become more significant when the microbial biomass P pool is enriched by organic matter.

Conceptual model of macrophyte-mediated phosphorus cycle

It should be emphasized that macrophyte biomass can generate a very high second P pool in addition to that of the sediment (Marion and Paillisson 2003). Upon reflooding, plant P release was intensified under anaerobic conditions and higher when dried sediments showed reduced P retention (or released more P themselves). Based on our findings, we schematically described P cycling in the Itaparica Reservoir influenced by intense wet–dry cycles and associated macrophyte dieback (Fig. 7). Heavy rainfall in the upper reaches of the São Francisco River is the major source of P for the reservoir and is characteristic of the end of the rainy season. The dominating macrophyte, *Egeria*, is capable of a C4-like metabolism (Casati et al. 2000) and grows very quickly. The high P uptake rates and P use efficiency of *Egeria* results in the rapid translocation of imported P into *Egeria* biomass. In the Itaparica Reservoir, where the growing season is all along the year, *Egeria* is an effective P sink and can hold 10 times more P than the surface sediment. The risk of sediment resuspension in newly exposed littoral areas increases when water levels decline. Therefore, when the water level is low and lake volume is reduced, the surface water can show elevated P concentrations. The lowered water level induces water stress for submersed macrophytes and can result in senescence in the shallower littoral areas. The translocation of P from water and

sediment into macrophyte biomass declines as a result of reduced growth. Furthermore, the first release of plant P may be the result of leaching and mineralization of plant litter. Large littoral areas are exposed during the prolonged desiccation period. Dry and mineralized surface sediments are vulnerable to wind erosion. Both processes can result in increased P input into the water. The affinity and capacity of the sediment to take up P is altered by prolonged desiccation, both by the oxidation of sediments (due to cracks and fissures also found in deeper layers) promoting the availability of Fe-oxides as P binding sites, and also by mineral aging and sediment compaction, which can result in a lowered surface area and a reduction in P binding sites. An increased risk of macrophyte dieback is the result of extended water stress during exposure. When the water supply increases, the reflooding of desiccation areas results in the quick release of P from mineralized sediments and macrophyte litter, and a pulse of readily bio-available P to the water is the consequence. The decomposition of plant litter can promote the release of redox-sensitive P from sediments or impair Fe-coupled sediment P retention. The desiccation-induced reduction of *Egeria* biomass results in a lowered P uptake rate by the macrophytes. The reduced growth inhibits the accumulation of the released P and leaves the mobilized P available for algal bloom development and toxin-producing cyanobacteria formation. After reflooding and during the subsequent succession, *Egeria* populations re-occupy the sites affected by drying and incorporate P in their biomass. *Egeria* turns back into a P sink; the regime can shift from a potentially phytoplankton-dominated regime to a state of macrophyte domination and increased water transparency. Thereby, *Egeria* represents an important pathway for P cycling and WLF can determine the source–sink relation of *Egeria* and sediments in the system. Especially shallow reservoir branches with a high water residence time such as Icó-

Fig. 7 Proposed effect of water level fluctuations on macrophyte growth and sediment drying in shallow areas and influence on benthic phosphorus (P) cycling. *Bold text within boxes and bold connections between boxes indicate dominating processes. Plus sign indicates P that is mobilized and released to the surface water, and minus sign indicates P removal from the water or reduced mobilization*



Mandantes Bay are therefore subjected to an accumulation of nutrients and can turn into eutrophication hotspots.

Impact of water level fluctuations on phosphorus load

To estimate the potential impact on P mobilization, we scaled up the P release based on the mesocosm experiments to the level Icó-Mandantes Bay in the Itaparica Reservoir. The area which is a potential habitat for *Egeria* and is affected by WLF and consequently can become completely dry constitutes up to 12 km². With 380–510 g *Egeria* biomass (dw) per m², the P content of the plants adds up to 59–79 t or 4.9–6.5 g P per m² of vegetated desiccation area. For the whole bay (including unvegetated sites), the P load that can enter the surface water after reflooding accounts for 2.3–3.1 g per m². In our experiment, we found that (1) maximal 10 % of plant-TP was released to the surface water as SRP, and (2) that the high sediment affinity for P uptake, although reduced after drying/reflooding, further reduced the release of plant-TP to the water to 4 %. Accordingly, the potential SRP load that is generated by *Egeria* corresponds to 0.09–0.13 g SRP per m² when calculated for the whole bay. The critical TP concentration for considerable phytoplankton development and a potential shift in water quality to eutrophic conditions according to the Organisation for European Co-operation and Development (OECD) standards) was estimated at 25 µg TP L⁻¹ for the Itaparica Reservoir (Selge et al. 2015). This shows that the reservoir reacts in a very sensitive manner towards increased P loads. Although our data describe a single, short-term pollution event and eutrophication thresholds are normally based on annual averages, readily available *Egeria*-P, which enters the surface water after reflooding, can be of significance. Therefore, the short time in which WLF affect P release and lead to elevated concentrations in the water is crucial. Frequent WLF may change the quality of littoral sediments over time. Sediments which have a history of drying and reflooding may react differently and lead to diverse results. Our results are therefore true for sediments that did not face wet–dry cycles before and can be used to describe initial biogeochemical alterations by WLF. Furthermore, our P load calculation is based on values derived in the laboratory and does not consider all parameters that affect P cycling in the reservoir (e.g., residence time, changes in sediment quality). However, the calculation demonstrates the important role of *Egeria* and WLF for P cycling. Our observations that WLF can release quick pulses of bioavailable P and affect productivity are in agreement with Kolding and van Zwieten (2012). The authors found that reservoirs which are subject to WLF are more productive than stable systems. Accordingly, unstable hydrodynamic conditions and the modification of water residence time can alter the nutrient availability (Rangel et al. 2012) and lead to a bottom-up driven increase in biological productivity.

Conclusion

Our results show the potential impact of WLF for water quality with reference to Icó-Mandantes Bay and the Itaparica Reservoir and provide new findings for water service management and dam operation. From an ecological short-term point of view, we suggest to minimize the (operational) amplitude of WLF whenever possible. Long sediment/macrophyte exposure and a long water residence time, in particular, can lead to significant nutrient accumulations upon rewetting, especially in isolated branches. A modification of reservoir volume towards minimal WLF may appear challenging and also depends on the natural water supply. Nevertheless, the prevention of strong WLF might repress the quick release of P into the water that is particularly observed after rapid refilling of reservoirs (Watts 2000a). In the Itaparica Reservoir, a stricter coupling of hydropower production to the natural water supply could reduce such impacts. *Egeria* is a significant sink for external P, and WLF can affect growth and thus P accumulation in the biomass. Besides quick P release from *Egeria* during wet–dry cycles, reduced *Egeria* growth and unchanged or increased external P input might therefore lead to slowly increasing P concentrations in the surface water. In this study, we found high *Egeria* standing stocks irrespective of season. The removal of desiccated macrophytes in times of sediment exposure is a proven method to withdraw nutrients from the system (Asaeda et al. 2000; Hilt et al. 2006; Zak et al. 2014) and can help to control P inputs and reduce water quality impairment when water levels increase (Watts 2000a). Effort, costs, and benefits, however, must be harmonized and the procedure must be repeated regularly when water levels are low because of the relatively aggressive vegetative growth and spread of *E. densa* (Wells and Clayton 1991, de Winton et al. 2009; Ribaudo et al. 2014). A further investigation of the usage of harvested *Egeria* (e.g., as fodder or for agricultural soil amelioration) might support the acceptance and implementation of such management measures among local stakeholders.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

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