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Nutrient release and uptake by littoral macrophytes during water level fluctuations

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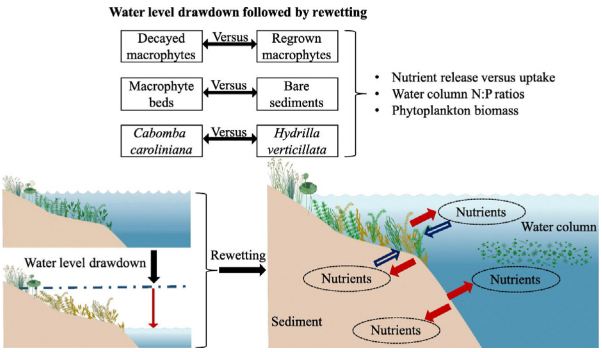
HIGHLIGHTS

- Comparison between macrophytes and sediments on nutrient release during WLFs
- Dried macrophytes had higher P impacts than bare dried-sediments after rewetting.
- Bare dried-sediments had higher N impacts than dried macrophytes after rewetting.
- Invasive macrophytes resulted in higher water quality deterioration than native one.s
- Regrown macrophytes are crucial in reducing nutrients after drying-rewetting.

GRAPHICAL ABSTRACT



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ABSTRACT

Water level drawdown followed by rewetting in reservoirs/lakes can shift macrophytes from a nutrient sink to a source, thus changing nutrient dynamics and causing water quality problems. However, there is limited understanding of the effect of macrophyte growth versus decomposition on nitrogen (N) and phosphorus (P) dynamics during water level fluctuations (WLFs). This study examined nutrient release versus uptake by two submerged macrophytes, the invasive *Cabomba caroliniana* (*Cabomba*) and the native *Hydrilla verticillata* (*Hydrilla*), compared to bare sediments, after drying then rewetting. Overall, we examined the nutrient dynamics in treatments comparing 1) two macrophyte species, 2) macrophyte nutrient uptake versus release, and 3) the presence of macrophytes versus bare sediments. Our study showed that *Cabomba* litter had a higher nutrient release rate and resulted in higher water column chlorophyll *a* concentrations compared with *Hydrilla* litter. The decomposition impact of both species on water column P concentrations was greater than that for N, and proportionally less P was assimilated than released by macrophytes compared with N. This resulted in P accumulation and a decreased N:P ratio in the water column compared to bare sediments without macrophytes. Phosphorus accumulation in the water column during macrophyte decomposition increased phytoplankton growth in our study, highlighting the potential for phytoplankton blooms, especially in P-deficient lakes. Regrown *Hydrilla* had a higher potential for assimilating sediment N compared to *Cabomba*. In contrast, regrown *Cabomba* was more efficient at reducing water column N compared with *Hydrilla*, suggesting different pathways of assimilation. Neither regrown *Cabomba* nor *Hydrilla* significantly reduced water column P concentrations. This study highlights different nutrient impacts of macrophyte beds compared to bare sediments during WLFs, and the role of regrown macrophytes in assimilating the released nutrients from macrophyte decomposition. However, the scale of their role is dependent on macrophyte species, forms of nutrients and drying-wetting regimes.

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1. Introduction

Rooted submerged macrophytes play a vital role in nutrient cycling and dynamics in the littoral zone of aquatic ecosystems and can utilize nutrients from both sediments and the water column (Madsen and Cedergreen, 2002; Barko et al., 1991). Macrophytes are regarded as an important nutrient sink in shallow freshwater ecosystems. However, their role as a nutrient sink can be reversed if they die and subsequently release nutrients when rewetted (Li et al., 2014; Lu et al., 2017b).

Water level fluctuations (WLFs) are one of the most important physical processes that cause the death of macrophytes, subsequently affecting nutrient cycling in the littoral zone. WLFs can be driven by natural fluctuations in rainfall and runoff, or in the case of reservoirs, also due to water abstraction or flood control. Reservoirs, therefore, can suffer more WLFs than natural lakes. Moreover, water quality deterioration has become a major threat for reservoirs that supply drinking and irrigation water and other human water uses, and this is likely to be worse during WLFs (Cooke et al., 2005; Gunkel and Sobral, 2013; Keitel et al., 2016). Global climate change is also likely to exacerbate WLFs with more prolonged droughts and intense floods becoming more frequent (Dai, 2011; Hirabayashi et al., 2008; Wantzen et al., 2008).

Submerged macrophytes can also recover from WLFs after rewetting depending on the duration of water level drawdown. *Re*-germination from seeds or dormant propagules provide a mechanism as these are more drought resistant than the aboveground biomass and other vegetative propagules (Bornette and Puijalon, 2011; Liu et al., 2006). Shoot fragments carried in the water column can also provide a rapid way for macrophytes to recover (Barrat-Segretain and Bornette, 2000). The regrown submerged macrophytes can then uptake the released nutrients from decayed macrophytes, and compete with phytoplankton for both nutrients and light (Scheffer et al., 1993; Søndergaard and Moss, 1998). Therefore, quantifying the relative importance of macrophytes as a nutrient sink or source during WLFs in shallow freshwater ecosystems is important in determining the effect of WLFs on water quality. However, this has not been well quantified in previous studies.

In this study, we investigated the relative importance of nutrient release from macrophyte litter versus nutrient uptake by living macrophytes (regrown from shoot fragments), and the effect on water quality during a cycle of drying then rewetting. We compared the impacts in an invasive (*Cabomba caroliniana*) and a native species (*Hydrilla verticillata*). We also examined the impacts of macrophyte bed desiccation on water quality upon rewetting, compared with a bare sediment treatment.

2. Methods

2.1. Macrophyte litter preparation

Healthy shoots of *C. caroliniana* (*Cabomba*) and *H. verticillata* (*Hydrilla*) were collected from two subtropical reservoirs, Ewen Maddock reservoir (26.6808° S, 153.0061° E) and Wyaralong reservoir (27.9092° S, 152.8811° E) in southeast Queensland, Australia. Macrophyte shoots were washed thoroughly with tap water in the laboratory (for details see Lu et al., 2017a).

Macrophytes were then labelled with ^{15}N (sodium nitrate: Na^{15}NO$_3$; ^{15}N: 99.9%) by cultivation in a ^{15}N–labelled nutrient solution for two weeks. The ^{15}N–labelled macrophyte litter was used to trace the fate of nitrogen (N) from macrophyte decomposition after drying then rewetting in mesocosms, and detailed methods are outlined in Lu et al. (2017a). Since the results of the ^{15}N tracer study were published elsewhere (Lu et al., 2017a), here we report on additional results from the same experiment which do not include the tracer results.

We investigated the relative importance of 1) nutrient (N and phosphorus) release from macrophyte litter versus 2) nutrient uptake from living macrophytes, by having treatments with and without: 1) macrophyte litter and 2) living macrophytes (Fig. 1). The macrophyte litter used in this experiment was dried macrophytes that harvested from the cultivated macrophyte shoots. The harvested macrophytes were cut into 10 cm fragments and oven dried at 50 °C to a constant weight. A total dry biomass of 2.5 g of each species (*Cabomba* or *Hydrilla*) was packed into each litter bag (width: 5 cm; length: 10 cm; pore size: 2 mm) for the subsequent decomposition experiment followed by rewetting. These litter bags were then added to mesocosms with different drying-wetting regimes of sediments, and the presence and absence of living macrophytes.

2.2. Mesocosm drying-wetting regimes

The sediment added to mesocosms had two treatments: 1) dried then rewetted; and 2) constantly wet (see Lu et al., 2017a). The dried then rewetted treatment was designed to simulate the effect of water level drawdown followed by rewetting. Sediment samples were collected using a spade from the surface layer sediment (10 cm) in the littoral zone (water depth 5–10 cm) of Tingalpa Reservoir (27.5281° S, 153.1803° E) in southeast Queensland. Stones and plant roots were removed from the sediment before it was homogenized, then 800 g (wet weight) sediment was placed at the bottom of each of 128 plastic non-transparent mesocosms (5 L, diameter: 18 cm, height 20 cm). Half of the mesocosms ($n = 64$) were dried for ten weeks in a glasshouse (mean temperature 30 ± 4 °C). The remaining mesocosms ($n = 64$) were kept in the same glasshouse, but saturated using a weekly addition of 300 mL of deionized water (water depth < 0.5 cm). After this 10-week period, a litter bag with either *Cabomba* or *Hydrilla* litter was added to each mesocosm and anchored to the sediment with stones. In summary, there were four treatments containing either *Cabomba* or *Hydrilla* litter combined with either "constantly wet" or "previously dried" sediment (Fig. 1).

These mesocosms were then refilled with diluted reservoir water (4 L each) to commence the litter leaching process. The reservoir water was collected from the surface water (20 cm) in Tingalpa Reservoir, then well mixed with deionized water at a volume ratio of 1:3 (reservoir water to deionized water). The water column in each mesocosm remained static without aeration before each sampling occasion.

2.3. The presence of living macrophytes

To investigate the nutrient assimilation by regrown macrophyte from shoot fragments as a result of litter decomposition, healthy shoots (6 g wet weight) of living *Cabomba* or *Hydrilla* were added to half of the mesocosms and left floating in the water column at the beginning of the refilling period. The macrophyte shoots were left floating, rather than planted to the sediment, to reduce the disturbance to the sediment and nutrient release. The floating macrophyte shoots started to grow new roots 3 d after rewetting and gradually anchored into the sediment.

The experimental design, therefore, tested three main effects: 1 - litter species - *Cabomba* (C) versus *Hydrilla* (H); 2 - sediment desiccation history - "dried then rewetted" (D) versus "constantly wet" (W); 3 - living macrophyte shoots - presence of *Cabomba* or *Hydrilla* shoots versus absence of shoots (Cs, Hs, or none). These treatments were combined to give eight specific treatments (Fig. 1): 1. dried-rewetted sediments + *Cabomba* litter (DC); 2. dried-rewetted sediments + *Cabomba* litter + living *Cabomba* shoots (DCCs); 3. constantly wet sediments + *Cabomba* litter (WC);4. constantly wet sediments + *Cabomba* litter + living *Cabomba* shoots (WCCs); 5. dried-rewetted sediments + *Hydrilla* litter (DH); 6. dried-rewetted sediments + *Hydrilla* litter + living *Hydrilla* shoots (DHHs); 7. constantly wet sediments + *Hydrilla* litter (WH); and 8. constantly wet sediments + *Hydrilla* litter + living *Hydrilla* shoots (WHHs). There were four rewetting periods (3, 7, 14, and 28 d after rewetting) for each treatment, each with four replicates.

Six extra mesocosms without macrophyte litter or living macrophyte shoots were also set up with sediment as the control treatments,