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Effects of water level fluctuations on nitrogen dynamics in littoral macrophytes

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Abstract

Sustained water level drawdown followed by rewetting has the potential to shift macrophytes from a nutrient sink to a source, but the fate of macrophyte-derived nutrients after rewetting is not well understood. We investigated the fate of released nitrogen (N) from isotopically labeled macrophyte litter over a 4-week period after rewetting. We used three treatments: (1) different species in the litter (invasive *Cabomba caroliniana* vs. native *Hydrilla verticillata*); (2) sediment desiccation history (“dried then rewetted” vs. “constantly wet”); (3) living macrophytes (presence vs. absence). Our results showed that the *Cabomba* litter treatment had a significantly higher percentage of macrophyte-derived ^{15}N in the dissolved fraction of the water column and assimilated by phytoplankton (higher chlorophyll *a* concentrations), compared to the *Hydrilla* litter. The treatments with sediment desiccation also had a significantly higher percentage of ^{15}N in the dissolved fraction and used by phytoplankton after rewetting, but less in the sediment, compared to the constantly wet treatment. The presence of living macrophytes partially reduced the ^{15}N increase in the water column and/or sediment, but the scale of the effect was species- and biomass-dependent. Our study showed that sediment pre-desiccation changed the fate of macrophyte-derived ^{15}N after rewetting, increasing the impact on water quality. This was further exacerbated by the presence of litter from an invasive species. This study highlights the need to manage water levels to maintain healthy macrophyte beds and thereby addressing water quality issues in lakes and reservoirs.

Submerged macrophytes play a key role in assimilating and storing nutrients and controlling phytoplankton blooms as they compete with phytoplankton for nutrients and light (van Donk et al. 1993; Van Donk and Van de Bund 2002). However, this role of macrophytes could be offset during periods of plant die-back when decomposition processes result in nutrient release (Li et al. 2014).

Water level fluctuations (WLFs) can lead to water quality deterioration through the nutrient release from rewetting the desiccated sediments and macrophytes in the littoral zone. Rewetting after drying can result in significant nitrogen (N) and carbon dioxide release from previously desiccated sediments, which has been known as the “Birch effect” (Birch 1958). We have also demonstrated that water level drawdown has the potential to shift macrophyte beds from a nutrient sink to a source after rewetting (Lu et al. 2017). Nutrients released from sediments or decayed macrophytes might become a direct nutrient source for phytoplankton growth. This water quality deterioration during WLFs is a

particular issue in areas where frequent hydrological changes occur due to droughts or floods (Beklioglu and Tan 2008; Romo et al. 2013), and in reservoirs where water levels are affected by water demand for human uses (Zohary and Ostrovsky 2011; Rangel et al. 2012). WLFs are likely to become more extreme with global climate change affecting weather conditions, e.g., more frequent droughts and floods (Hirabayashi et al. 2008; Dai 2011; Callieri et al. 2014).

Macrophyte species may vary in their impacts on water quality during WLFs due to various nutrient uptake/release capabilities and the density of canopy they can form (Frodge et al. 1990). Invasive species, for example, are more likely to form a dense canopy that reduces oxygen exchange and biodiversity, compared to native species (Schooler et al. 2006; Schooler 2009). These invasive species typically have rapid growth and high adaptability to a range of environmental conditions so that they can out-compete native species (Blumenthal and Hufbauer 2007). Therefore, invasive species are expected to have more nutrient storage than native species, but also release more nutrients when drying and rewetting events occur.

Desiccated macrophyte beds are also capable of recovering after rewetting, mainly by the germination from roots or seeds, or by the growth of shoot fragments in the water column (Thomaz et al. 2006). These regrown submerged

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macrophytes can utilize nutrients from both the water column and sediments (Carignan 1982; Chambers et al. 1989; Madsen and Cedergreen 2002), thus might alleviate the water deterioration from macrophyte decomposition. However, the fate of these released nutrients from desiccated macrophytes as a result of WLFs, as well as the impact of regrown macrophytes on utilizing these released nutrients are poorly understood. For example, it is unclear whether these released nutrients are stored in the sediment, re-assimilated by regrown macrophytes, cycled through the water column or released to the atmosphere, and whether these nutrients become available to phytoplankton.

Sediment desiccation has been found to increase the regrowth of macrophytes due to the increased nutrient availability in systems after rewetting, thus impacting the fate of nutrients released from macrophyte decomposition (Barko et al. 1986; James et al. 2004). Sediment desiccation might also affect the nutrient dynamics through interfering microbial activities or redox conditions, such as increasing nitrification process by providing energy (carbon), substances (ammonium) and oxidation conditions for nitrifiers after rewetting, or slow down microbial activities after severe drawdown conditions (Qiu and McComb 1996; Baldwin and Mitchell 2000).

There has been increasing evidence of N limitation for phytoplankton growth in freshwater ecosystems (e.g., Cavanaugh et al. 2006; Elser et al. 2007). The substantial N released from macrophyte beds after drying then rewetting, therefore, could be a significant trigger for phytoplankton blooms in N-deficient lakes or reservoirs. Stable nitrogen isotope (^{15}N) tracing techniques can be used to investigate N cycling processes in aquatic ecosystems, such as the N assimilation by phytoplankton or periphyton (Neess et al. 1962; Glibert et al. 1982; Axler and Reuter 1996), the transformation of N inputs in food-webs (Hadwen and Bunn 2005), and the denitrification in lake sediments (Nielsen 1992; Risgaard-Petersen and Jensen 1997) or in wetlands (Mofizur et al. 2015). This technique has also been used in forests or farmlands to determine the fate of plant-derived N (Müller and Sundman 1988; Zeller et al. 2000).

In this study, we used ^{15}N tracing techniques to examine the fate of macrophyte-derived N upon rewetting following a drying event. We aimed to investigate: (1) if species differences in the litter, i.e., *Cabomba caroliniana* (invasive) and *Hydrilla verticillata* (native), will have different impacts on N dynamics upon rewetting; (2) the effect of living submerged macrophytes on the fate of N derived from macrophyte litter; and (3) the effect of sediment desiccation history on the fate of N derived from macrophyte litter.

Methods

Labeling of submerged macrophytes with ^{15}N

Healthy shoots of *C. caroliniana* (*Cabomba*) and *H. verticillata* (*Hydrilla*) were collected from Ewen Maddock reservoir

(26.6808° S, 153.0061° E) and Wyaralong reservoir (27.9092° S, 152.8811° E), respectively, in south-east Queensland, Australia. Macrophyte shoots were washed thoroughly with tap water in the laboratory to remove any attached periphyton and were subsequently cultivated in the laboratory in a ^{15}N -labeled nutrient solution.

A 2000-liter water tank (diameter: 190 cm; height: 90 cm) was used for macrophyte cultivation. The tank was cleaned with sodium dichloroisocyanurate, filled with tap water, and left in natural sunlight for a week to remove the chlorine. The macrophyte shoots (length: 30 cm) were secured on a plastic mesh by cable ties and anchored to the bottom of the tank by stones. A ^{15}N -labeled nutrient solution was made up according to the modified one-fifth strength standard Hoagland nutrient solution (Hoagland 1937), including N (from sodium nitrate: $\text{Na}^{15}\text{NO}_3$; ^{15}N : 99.9%, 0.42 mg $^{15}\text{N L}^{-1}$), P (0.06 mg P L^{-1}), potassium, magnesium, iron, and other micronutrients. The nutrient solution was added to the tank every week to ensure macrophytes had sufficient nutrients for growth, and to achieve the desired level of ^{15}N enrichment. Each species was cultivated separately in the tank for 2 weeks. The final ^{15}N ratio in macrophyte biomass was 2.5 atom% for *Cabomba* and 4.0 atom% for *Hydrilla*.

After 2 weeks of cultivation, the ^{15}N -labeled *Cabomba* and *Hydrilla* were harvested, cut into 10 cm fragments and mixed well. Subsamples of each species were oven-dried at 50°C to a constant weight, and 2.5 g of dry biomass was packed into each litter bag (width: 5 cm; length: 10 cm; pore size: 2 mm). Total carbon and total nitrogen (TN) content in *Cabomba* and *Hydrilla* litter were measured using a stable isotope ratio mass spectrometer (Sercon Hydra 20–22, Sercon, UK), with a front sample combustion system (Euro EA-GLS elemental analyzer, Sercon, UK). The C : N ratio was then calculated in macrophyte litter.

Experimental design for sediment desiccation

The litter bags were placed in mesocosms with two sediment treatments prior to commencing the experiment, i.e., the dried then rewetted sediment and the constantly wet sediment treatments. The dried then rewetted treatment was to simulate the effect of water level drawdown followed by rewetting. Fresh sediment was collected from the surface (10 cm) of the littoral zone (water depth 5–10 cm) of Tingalpa Reservoir (27.5281° S, 153.1803° E) in south-east Queensland using a spade. The sediment was well mixed to homogenize and remove stones and plant roots, then sediment samples (800 g wet weight each) were placed in the bottom of 128 plastic non-transparent mesocosms (5 L, diameter: 18 cm, height 20 cm). Half of the mesocosms ($n = 64$) were dried for 10 weeks in a glasshouse (mean temperature $30 \pm 4^\circ\text{C}$) to reach a minimum soil moisture around 1.1%. The remaining mesocosms ($n = 64$) were kept saturated by adding 300 mL deionized water weekly (water depth < 0.5 cm). After this 10-week period, a litter bag with either ^{15}N -labeled *Cabomba* (C) or *Hydrilla* (H) was added

Table 1. Experimental design. Sampling occasions for each treatment were 3 d, 7 d, 14 d, and 28 d after rewetting. Four replicates were used for each treatment.

Codes for the eight specific treatments	Species in the litter	Sediment desiccation	Addition of living macrophytes
DC	<i>Cabomba</i>	+	–
DCCs	<i>Cabomba</i>	+	+
WC	<i>Cabomba</i>	–	–
WCCs	<i>Cabomba</i>	–	+
DH	<i>Hydrilla</i>	+	–
DHHs	<i>Hydrilla</i>	+	+
WH	<i>Hydrilla</i>	–	–
WHHs	<i>Hydrilla</i>	–	+

to each mesocosm and anchored to the sediment with stones. Therefore, the treatments consisted of “constantly wet” (WC: wet sediment + *Cabomba* litter or WH: wet sediment + *Hydrilla* litter) and “previously dried” (DC: dried sediment + *Cabomba* litter or DH: dried sediment + *Hydrilla* litter) sediment, containing either *Cabomba* or *Hydrilla* litter.

Mesocosm set-up and sampling methods

One liter of surface reservoir water, sampled from Tingalpa Reservoir (27.5281° S, 153.1803° E), was mixed with 3 L of deionized water and added to each mesocosm of all treatments (both the “constantly wet” and “previously dried” sediment treatments). To investigate the impact of macrophyte regrowth on the fate of ^{15}N , half of the treatments had 6 g (wet biomass) of healthy living *Cabomba* or *Hydrilla* shoot fragments added (Cs or Hs) into the water column. Therefore, the experiment had three main treatments, i.e., treatment 1 (T1): different species in the litter (*Cabomba* vs. *Hydrilla*); T2: sediment desiccation history (“dried then rewetted” vs. “constantly wet”); T3: living macrophytes (presence vs. absence). The three main treatments consisted of eight specific treatments, WC, WCCs (wet sediment + *Cabomba* litter + living *Cabomba* shoots), DC, and DCCs (dried sediment + *Cabomba* litter + living *Cabomba* shoots) for *Cabomba* and WH, WHHs (wet sediment + *Hydrilla* litter + living *Hydrilla* shoots), DH, and DHHs (dried sediment + *Hydrilla* litter + living *Hydrilla* shoots) for *Hydrilla*, each with 16 replicates (Table 1).

Samples of five major N pools from each mesocosm were taken from four replicates on day 3, 7, 14, and 28 after rewetting. These N pools were: particulate organic N (PON) in the water column; the total dissolved water column N without PON (dissolved fraction thereafter); the entire sediment in the mesocosm (well mixed); the living macrophyte regrown from fragments (regrown macrophytes thereafter); and the remaining macrophyte litter. PON samples were assumed to represent the phytoplankton N pool (Del Giorgio and France 1996). In addition, samples for ^{15}N -natural abundance measurement in

each pool were taken before rewetting the mesocosms when ^{15}N -labeled litter was not added.

Chlorophyll *a* (Chl *a*) concentrations and ^{15}N isotope ratios for PON samples were measured by filtering 100 mL of water samples onto pre-combusted (450°C, 4 h) glass fiber filters (47 mm diameter; GF75, Advantec, Japan). Filters for Chl *a* were frozen at –80°C until analyzed, while those for isotope analysis were oven-dried at 50°C to a constant weight. The supernatant from filtration (500 mL), which represented for the dissolved fraction of the water column, was frozen in wide mouth high-density polyethylene jars for subsequent freeze drying (VirTis-wizard 2.0, VWR, U.S.A.). The macrophyte litter in litter bags and the living macrophytes in each mesocosm were rinsed with deionized water and dried in an oven at 50°C to a constant weight. At the end of sampling, the entire sediment in each mesocosm was well mixed, subsampled, freeze-dried, and ground for ^{15}N analysis.

Water samples for total dissolved nitrogen (TDN) and phosphorus (TDP) concentrations were processed by filtering through membrane filters (0.45 μm pore size, Whatman). TDN and TDP were analyzed colorimetrically using Continuous Segmented Flow Analyzer (SEAL Auto Analyzer 3 HR, SEAL Analytical Limited, UK). Filters for Chl *a* were cut into small pieces first and sonicated in 90% acetone for 1 min with a probe sonicator (Branson 450, U.S.A.). The sonicated extracts were kept at –20°C overnight maximizing the extraction of pigments, then extracts were filtered through glass fiber filters (GF75, Advantec, Japan) to remove particulates. Concentrations of Chl *a* were calculated using the trichromatic equations of Jeffrey and Welschmeyer (1997) after measuring the absorbance of the extracts at 750 nm, 665 nm, 664 nm, 647 nm, and 630 nm with a spectrophotometer (UV-2450 Shimadzu, Japan).

Total dry weights or volumes of each N pool were recorded for subsequent ^{15}N mass balance calculations. The water temperature in representative mesocosms and the ambient light intensity above mesocosms were recorded at a frequency of 30 min during the experiment using temperature loggers (Thermocron iButton, Maxim Integrated, California, U.S.A.) and a photosynthetic active radiation light logger (LI-1400, Nebraska, U.S.A.), respectively. The specific conductivity, dissolved oxygen (DO), pH, and turbidity in the water column in each mesocosm were measured around 17:00 h and 18:00 h on each sampling occasion using a calibrated Hydro-lab logger (Quanta, U.S.A.).

^{15}N analysis

Dried macrophyte and sediment samples were ground into fine (< 0.1 mm) homogenized powder using a RETSCH Mixer Mill (MM 400, GENEQ, Canada). Sub-samples (2–3 mg; approximately 50 μg N in each sample) of plant material, sediment, and freeze dried water samples, and one-eighth of each PON filter were weighed and folded into tin capsules for subsequent isotope analysis. TN content and $^{15}\text{N}/^{14}\text{N}$ ratios of all samples from treatments before and

after rewetting were measured using a stable isotope ratio mass spectrometer (Sercon Hydra 20–22, Sercon, UK), with a front sample combustion system (Euro EA-GLS elemental analyzer, Sercon, UK).

The mass balance for ^{15}N in each mesocosm was calculated using the amount of added ^{15}N , which was the subtraction between the total ^{15}N and the naturally occurring ^{15}N (calculated

from ^{15}N -natural abundance) in each pool. The ^{15}N -natural abundance in each N pool was measured from the samples before ^{15}N -labeled litter was added. Since *Cabomba* and *Hydrilla* litter had different ^{15}N enrichment levels after cultivation, the ^{15}N mass in each N pool in *Cabomba* or *Hydrilla* litter treatments were standardized to a percentage relative to the initial ^{15}N mass input: the percentage (%) of added ^{15}N (in each pool) =

$$\frac{\text{Additional } ^{15}\text{N mass in each pool}}{\text{Total input of additional } ^{15}\text{N mass in } \textit{Cabomba} \text{ or } \textit{Hydrilla} \text{ treatments}} * 100\%$$

Therefore, the relative importance of each N pool in the two macrophyte litter treatments can be compared using the standardized added ^{15}N percentage (% ^{15}N thereafter). The recovery of ^{15}N for each mesocosm was the total % ^{15}N of all quantified N pools. The residual ^{15}N was the total of unquantified N pools, i.e., the subtraction between 100% and the recovered % ^{15}N .

Data analysis

Data were analyzed using R software (version 3.12, R Core Team 2014). A general linear model (GLM) was used to compare the differences of standardized added ^{15}N percentage (% ^{15}N) transferred to each N pool and the total recovery of ^{15}N in each mesocosm among the eight specific treatments (DC, DCCs, WC, WCCs, DH, DHHs, WH, and WHHs). For each parameter, four fixed variables were applied in the linear model, i.e., T1: macrophyte species in the litter (*Cabomba* vs. *Hydrilla*); T2: sediment desiccation history (“dried then rewetted” vs. “constantly wet”); T3: living macrophytes (presence vs. absence); T4: rewetting periods. Sum of squares for T1, T2, and T3 in each model were calculated to compare the relative magnitude of the significant differences among the three treatments. The interactions between T1, T2, and T3, and their interactions with rewetting periods were also applied in the linear model. However, the interaction terms among T1, T2, and T3 were dropped from the model for the N pool of dissolved fraction, PON, sediment, and the litter as they did not significantly improve the model. The differences among T1, T2, and T3 for each N pool after each rewetting period were also compared using GLM.

GLM was also used to compare physio-chemical variables (specific conductivity, pH, DO, and turbidity), water column Chl *a* concentrations, water column TDN and TDP concentrations, and TN and total biomass lost from *Cabomba* and *Hydrilla* litter among the eight specific treatments. The comparison of nutrient concentrations in the water column was based on nutrients leaching from the same dry biomass of *Cabomba* and *Hydrilla* litter. A two-way analysis of variance (ANOVA) was used to determine the effect of macrophyte species and the sediment desiccation process on the biomass increase of living macrophytes after each rewetting period.

Data were tested for normality and natural log-transformed as required.

Results

Physio-chemical and nutrient variables after rewetting

The mean daily temperature and daily-accumulated light quanta were $24.1 \pm 3.1^\circ\text{C}$ (SD) and $11.7 \pm 3.9 \text{ mol m}^{-2} \text{ d}^{-1}$, respectively, during the experiment. The C : N ratio in the *Cabomba* litter was 11 ± 2 , which was significantly lower than the *Hydrilla* litter (17 ± 5). The TN content in *Cabomba* litter (2.8%) was significantly higher than the *Hydrilla* litter (1.7%).

Across treatments, the treatment of “sediment desiccation history,” “species differences in the litter,” and “presence of living macrophytes (regrown macrophytes)” significantly affected the physio-chemical and nutrient variables in the water column after rewetting (Table 2). Specifically, the dried then rewetted sediment treatment significantly increased the water column specific conductivity, but significantly decreased the turbidity after rewetting, compared to the constantly wet sediment treatment for both *Cabomba* and *Hydrilla* treatments (GLM, $p < 0.05$; Table 2). The decomposition of *Cabomba* litter resulted in significantly lower DO concentrations and lower specific conductivity values, but higher turbidity, compared to that of the *Hydrilla* litter treatment. The regrowth of living *Cabomba* and *Hydrilla* significantly decreased specific conductivity and turbidity, but significantly increased DO concentrations in the water column (measurements were only done during the daytime). The value of pH was not significantly different among the eight specific treatments.

In general, the dried then rewetted sediment treatment had significantly higher TDN and TDP concentrations in the water column, compared to the constantly wet sediment treatment for both *Cabomba* and *Hydrilla* (GLM, $p < 0.05$; Fig. 1; Table 2). The TDN and TDP concentrations in the water column of *Hydrilla* treatments were significantly lower than that in *Cabomba* treatments, 14 d and 28 d after rewetting. The presence of regrown *Cabomba* significantly decreased water column TDN concentrations across the rewetting period, compared to the control with the absence of living *Cabomba*. In contrast, the presence of regrown *Hydrilla* only significantly

Table 2. The mean value ($\pm$ SD) of physio-chemical parameters, and TDP concentrations in the water column of the eight specific treatments after rewetting (on days 0, 3, 7, 14, and 28). Codes for treatment abbreviations explained in Table 1.

Codes	Days after rewetting	Cond. (mS cm ⁻¹)	DO (mg L ⁻¹)	pH	Turbidity (NTU)	TDP (mg P L ⁻¹)
DC	0	0.05 $\pm$ 0.01	6.88 $\pm$ 0.25	6.43 $\pm$ 0.02	5.23 $\pm$ 1.25	0.01 $\pm$ 0.00
	3	0.25 $\pm$ 0.01	3.86 $\pm$ 0.49	6.91 $\pm$ 0.11	23.05 $\pm$ 4.65	0.19 $\pm$ 0.06
	7	0.36 $\pm$ 0.01	4.03 $\pm$ 1.19	5.51 $\pm$ 0.15	87.33 $\pm$ 25.33	0.05 $\pm$ 0.01
	14	0.34 $\pm$ 0.01	3.22 $\pm$ 0.65	7.09 $\pm$ 0.01	48.03 $\pm$ 18.29	0.04 $\pm$ 0.00
	28	0.29 $\pm$ 0.02	3.09 $\pm$ 0.11	7.27 $\pm$ 0.04	50.55 $\pm$ 34.81	0.01 $\pm$ 0.00
WC	0	0.05 $\pm$ 0.01	6.88 $\pm$ 0.25	6.58 $\pm$ 0.02	5.23 $\pm$ 1.25	0.01 $\pm$ 0.00
	3	0.50 $\pm$ 0.02	3.64 $\pm$ 0.61	7.25 $\pm$ 0.01	64.78 $\pm$ 21.01	0.11 $\pm$ 0.08
	7	0.29 $\pm$ 0.02	3.03 $\pm$ 0.81	7.32 $\pm$ 0.02	126.35 $\pm$ 58.92	0.05 $\pm$ 0.01
	14	0.28 $\pm$ 0.01	2.52 $\pm$ 1.08	7.15 $\pm$ 0.03	99.53 $\pm$ 42.40	0.02 $\pm$ 0.01
	28	0.26 $\pm$ 0.01	2.95 $\pm$ 0.27	7.20 $\pm$ 0.01	75.48 $\pm$ 30.51	0.03 $\pm$ 0.01
DCCs	0	0.05 $\pm$ 0.01	6.88 $\pm$ 0.25	6.43 $\pm$ 0.02	5.23 $\pm$ 1.25	0.01 $\pm$ 0.00
	3	0.24 $\pm$ 0.02	6.55 $\pm$ 0.30	7.11 $\pm$ 0.07	30.20 $\pm$ 6.24	0.29 $\pm$ 0.06
	7	0.31 $\pm$ 0.01	5.06 $\pm$ 0.58	7.21 $\pm$ 0.06	34.88 $\pm$ 4.36	0.18 $\pm$ 0.03
	14	0.33 $\pm$ 0.01	4.81 $\pm$ 0.15	7.06 $\pm$ 0.09	22.70 $\pm$ 3.91	0.02 $\pm$ 0.01
	28	0.28 $\pm$ 0.01	2.94 $\pm$ 0.13	7.23 $\pm$ 0.02	26.93 $\pm$ 2.21	0.02 $\pm$ 0.00
WCCs	0	0.05 $\pm$ 0.01	6.88 $\pm$ 0.25	6.58 $\pm$ 0.02	5.23 $\pm$ 1.25	0.01 $\pm$ 0.00
	3	0.22 $\pm$ 0.01	6.68 $\pm$ 0.55	7.22 $\pm$ 0.04	43.03 $\pm$ 11.09	0.24 $\pm$ 0.08
	7	0.29 $\pm$ 0.02	6.43 $\pm$ 0.91	7.01 $\pm$ 0.15	100.98 $\pm$ 31.83	0.10 $\pm$ 0.05
	14	0.26 $\pm$ 0.02	4.13 $\pm$ 0.21	6.75 $\pm$ 0.12	124.43 $\pm$ 59.5	0.02 $\pm$ 0.01
	28	0.23 $\pm$ 0.04	2.94 $\pm$ 0.09	7.21 $\pm$ 0.03	146.40 $\pm$ 55.21	0.01 $\pm$ 0.00
DH	0	0.05 $\pm$ 0.01	6.88 $\pm$ 0.25	6.43 $\pm$ 0.02	5.23 $\pm$ 1.25	0.01 $\pm$ 0.00
	3	0.31 $\pm$ 0.02	3.22 $\pm$ 0.78	6.97 $\pm$ 0.01	11.48 $\pm$ 7.62	0.04 $\pm$ 0.01
	7	0.43 $\pm$ 0.02	2.49 $\pm$ 0.53	7.16 $\pm$ 0.02	32.23 $\pm$ 12.64	0.03 $\pm$ 0.01
	14	0.40 $\pm$ 0.01	3.68 $\pm$ 1.03	7.18 $\pm$ 0.02	41.65 $\pm$ 16.30	0.03 $\pm$ 0.01
	28	0.35 $\pm$ 0.02	0.36 $\pm$ 0.67	7.63 $\pm$ 0.03	56.10 $\pm$ 30.44	0.03 $\pm$ 0.01
WH	0	0.05 $\pm$ 0.01	6.88 $\pm$ 0.25	6.43 $\pm$ 0.02	5.23 $\pm$ 1.25	0.01 $\pm$ 0.00
	3	0.25 $\pm$ 0.02	4.73 $\pm$ 0.04	7.05 $\pm$ 0.02	22.80 $\pm$ 6.79	0.02 $\pm$ 0.00
	7	0.29 $\pm$ 0.01	3.33 $\pm$ 0.31	7.34 $\pm$ 0.07	51.93 $\pm$ 24.82	0.01 $\pm$ 0.00
	14	0.31 $\pm$ 0.01	4.21 $\pm$ 0.75	7.22 $\pm$ 0.03	96.45 $\pm$ 51.30	0.02 $\pm$ 0.01
	28	0.28 $\pm$ 0.02	4.68 $\pm$ 0.41	7.64 $\pm$ 0.03	101.68 $\pm$ 52.60	0.02 $\pm$ 0.01
DHHs	0	0.05 $\pm$ 0.01	6.88 $\pm$ 0.25	6.43 $\pm$ 0.02	5.23 $\pm$ 1.25	0.01 $\pm$ 0.00
	3	0.33 $\pm$ 0.04	3.92 $\pm$ 0.58	6.67 $\pm$ 0.15	8.15 $\pm$ 4.94	0.04 $\pm$ 0.00
	7	0.44 $\pm$ 0.02	2.97 $\pm$ 0.09	6.86 $\pm$ 0.23	24.55 $\pm$ 6.55	0.04 $\pm$ 0.01
	14	0.33 $\pm$ 0.02	7.35 $\pm$ 0.35	7.13 $\pm$ 0.08	35.00 $\pm$ 8.12	0.02 $\pm$ 0.01
	28	0.27 $\pm$ 0.02	7.50 $\pm$ 0.21	7.79 $\pm$ 0.10	24.85 $\pm$ 8.37	0.01 $\pm$ 0.00
WHHs	0	0.05 $\pm$ 0.01	6.88 $\pm$ 0.25	6.58 $\pm$ 0.02	5.23 $\pm$ 1.25	0.01 $\pm$ 0.01
	3	0.25 $\pm$ 0.02	4.90 $\pm$ 0.27	6.97 $\pm$ 0.05	13.33 $\pm$ 4.36	0.02 $\pm$ 0.01
	7	0.28 $\pm$ 0.02	3.26 $\pm$ 0.11	7.32 $\pm$ 0.11	70.25 $\pm$ 25.48	0.01 $\pm$ 0.00
	14	0.27 $\pm$ 0.02	6.52 $\pm$ 0.44	7.26 $\pm$ 0.44	67.40 $\pm$ 39.95	0.01 $\pm$ 0.01
	28	0.26 $\pm$ 0.02	6.35 $\pm$ 0.47	7.80 $\pm$ 0.47	68.23 $\pm$ 45.86	0.01 $\pm$ 0.00

Cond., specific conductivity; NTU, nephelometric turbidity unit.

reduced water column TDN and TDP concentrations 28 d after rewetting, compared to the control without living *Hydrilla*.

Time effects of rewetting on the fate of macrophyte-derived ¹⁵N

The ¹⁵N distribution among N pools after rewetting changed over time. Generally, the added %¹⁵N of macrophyte-derived

¹⁵N released into the dissolved fraction of the water column (dissolved fraction) and stored in the PON was highest 3–7 d after rewetting for both *Cabomba* and *Hydrilla* treatments (Table 3). The %¹⁵N then decreased with longer rewetting periods. In contrast, the %¹⁵N transferred to the sediment and regrown macrophytes increased gradually during the 28 d of rewetting.

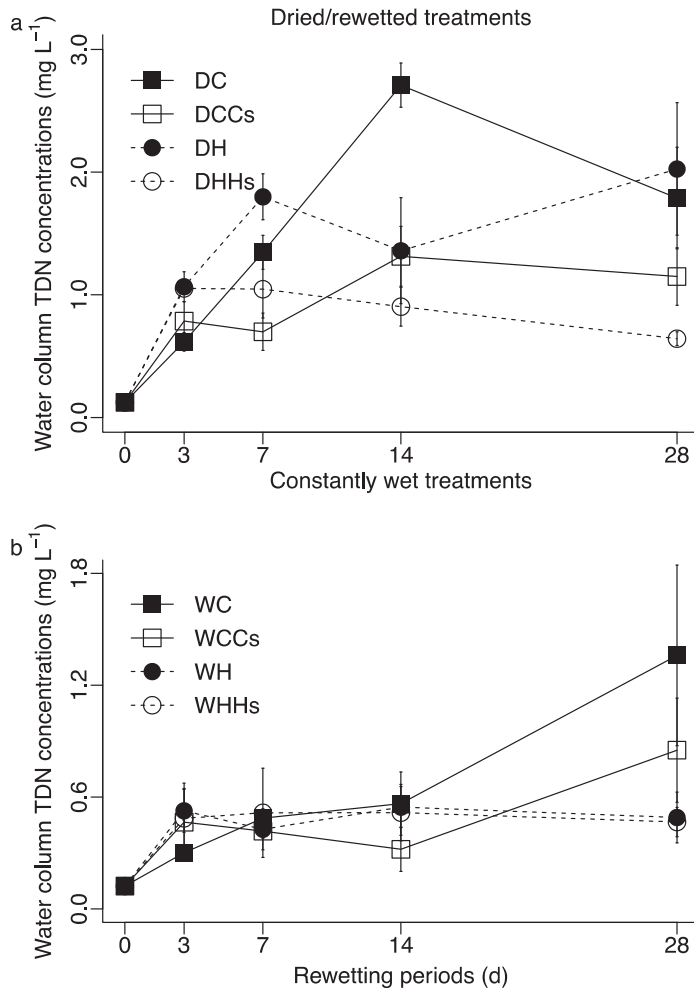


Fig. 1. The comparison of water column TDN concentrations between different litter species and the presence of living macrophytes in dried then rewetted (a) and constantly wet treatments (b), respectively.

Species differences in the litter on the fate of macrophyte-derived ^{15}N

The treatment of “species differences in the litter” explained more variation in the ^{15}N distribution in the pools of dissolved fraction, PON, and the residual N, compared to the other two treatments, i.e., “sediment desiccation history” and the “presence of living macrophytes” (Table 3). For instances, 28 d after rewetting, the $\%^{15}\text{N}$ released from *Cabomba* ($57.6\% \pm 9.1\%$) and *Hydrilla* litter ($54.1\% \pm 3.0\%$) in the dried then rewetted sediment treatment (i.e., DH and DC treatments) was not significantly different (GLM, $p > 0.05$; Fig. 2a,b). Although the same $\%^{15}\text{N}$ was released from each species, a significantly higher $\%^{15}\text{N}$ from *Cabomba* litter was transferred into the dissolved fraction ($3.9\% \pm 1.3\%$) and PON ($3.5\% \pm 3.8\%$) of the water column, compared to *Hydrilla* litter ($2.3\% \pm 0.5\%$ and $0.7\% \pm 0.4\%$, respectively; Fig. 2a,b). The residual ^{15}N for the DC treatment accounted for $19.4\% \pm 5.2\%$ of the total ^{15}N input

28 d after rewetting, which was significantly lower than $32.4\% \pm 3.3\%$ for the DH treatment.

The percentage of released TN (relative to total TN content in the biomass of macrophytes) was also different between *Cabomba* and *Hydrilla* litter after the same period of rewetting. A significantly higher percentage of the plant TN content was released from *Cabomba* litter ($53\% \pm 6\%$), compared to *Hydrilla* litter ($36\% \pm 10\%$), 28 d after rewetting (GLM, $p < 0.05$). There was also a significantly higher percentage of dry biomass lost from *Cabomba* litter ($60.3\% \pm 6.2\%$) than from *Hydrilla* litter ($43.9\% \pm 3.8\%$), 3 weeks after rewetting (GLM, $p < 0.05$).

Effects of sediment desiccation on the fate of macrophyte-derived ^{15}N

Sediment desiccation did not affect the total $\%^{15}\text{N}$ released from macrophyte litter 28 d after rewetting. However, sediment desiccation significantly altered the ^{15}N distribution in different N pools for both *Cabomba* and *Hydrilla* treatments (Table 3).

The treatment of “sediment desiccation history” explained more variation in the ^{15}N distribution in the sediment pool compared to the other two treatments, i.e., “species in the litter” and the “presence of living macrophytes” (Table 3). In general, the dried then rewetted sediment treatment had a significantly lower $\%^{15}\text{N}$ in the sediment pool, compared to the constantly wet sediment treatment. Instead, the dried then rewetted sediment treatment significantly increased the released ^{15}N transferring to the dissolved fraction and to the regrown macrophytes, compared to the constantly wet sediment treatment, for both *Cabomba* and *Hydrilla* treatments 28 d after rewetting (Table 3; Fig. 2c,d). The dried then rewetted sediment treatment also had a significantly higher $\%^{15}\text{N}$ transferred into the PON compared to the constantly wet sediment in the *Hydrilla* treatment.

Specifically, the dried then rewetted sediment treatment had 11.9% (*Cabomba*, DC) and 18.6% (*Hydrilla*, DH) less ^{15}N transferred to the sediment pool, compared to the constantly wet sediment treatment (WC and WH) 28 d after rewetting, but 1–2% more into the dissolved fraction of the water column (Fig. 2a–d). The regrown macrophytes in the dried then rewetted sediment treatment stored $3.2\% \pm 0.6\%$ (DCCs) and $5.1\% \pm 3.4\%$ (DHHs) more ^{15}N than the constantly wet sediment treatments for *Cabomba* (WCCs) and *Hydrilla* (WHHs) treatments, respectively (Fig. 2e–h).

For residual ^{15}N in mesocosms, there was an interaction between sediment desiccation history and species differences in the litter. For *Hydrilla* treatments, the residual $\%^{15}\text{N}$ was the highest in the dried then rewetted sediment treatment without living *Hydrilla* (DH), compared to all other treatments 28 d after rewetting (GLM, $p < 0.05$). The dried then rewetted sediment treatment for *Cabomba* also had a relatively higher residual ^{15}N , compared to all other treatments but the difference was not significant. (GLM, $p > 0.05$).

Table 3. Summary of statistical results (F values and significances) for the effect of different treatments on ^{15}N distribution in different N pools and water column TDN concentrations during rewetting periods.

		^{15}N pools						Water column TDN
Treatments (T)		Dissolved fraction	PON	Sediment	Living macrophytes		Residual ^{15}N	
					<i>Cabomba</i>	<i>Hydrilla</i>		
R^2 for the linear model		0.97	0.84	0.99	0.79	0.82	0.29	0.73
T1:	Species in the litter	140.98**	63.01**	103.83**	na	na	7.02**	5.05*
T2:	Sediment history	46.23**	3.84	214.96**	3.55	4.74*	3.54	56.16**
T3:	Living macrophytes	2.71	2.90	9.96**	197.41**	246.11**	0.41	4.26*
Sum of squares		T1>T2>T3	T1>T2>T3	T2>T1>T3	T3>T2	T3>T2	T1>T2>T3	T2>T1>T3
Rewetting periods	0 d	d	c	c	c	b	a	c
	3 d	a	a	b	bc	ab	c	b
	7 d	ab	a	b	bc	a	c	ab
	14 d	bc	ab	b	ab	a	b	ab
	28 d	c	b	a	a	a	c	ab

The * and ** indicate significant differences at $p < 0.05$ and $p < 0.01$ levels. The $\cdot$ indicates significant interaction between the treatment and rewetting periods at $p < 0.05$ level. Different lowercase letters (a, b, c, or d) indicate significant differences at $p < 0.05$ level between the five rewetting periods, ordered from "a" to "d" presenting the highest to the lowest treatment. Treatments which share a letter in common were not significantly different. na, not available.

Effects of macrophyte regrowth on the fate of macrophyte-derived ^{15}N

The regrown macrophytes were significant ^{15}N pools in both *Cabomba* and *Hydrilla* litter treatments. The "sediment desiccation history" treatment explained more variation in the ^{15}N distribution in the pool of regrown macrophytes, compared to the treatment of "species differences in the litter" (Table 3). The dried then rewetted sediment treatment had a significantly higher percentage of ^{15}N in the regrown macrophytes, compared to the constantly wet sediment treatment for both *Cabomba* and *Hydrilla* (GLM, $p < 0.05$). The ^{15}N taken up by regrown *Cabomba* accounted for $11.6\% \pm 2.2\%$ and $8.4\% \pm 2.8\%$ of the total ^{15}N input for DCCs and WCCs treatments, respectively, 28 d after rewetting (Fig. 2e,g). The ^{15}N assimilated by regrown *Hydrilla* took up $8.2\% \pm 4.1\%$ of added ^{15}N for the DHHs treatment, and $3.1\% \pm 0.7\%$ for the WHHs treatment 28 d after rewetting (Fig. 2f,h).

The presence of regrown macrophytes significantly decreased the ^{15}N distribution in other N pools, i.e., the sediment, the dissolved fraction, and PON. In addition, the effect of regrown macrophytes varied between species. Specifically, the regrown *Hydrilla* significantly reduced the $\%^{15}\text{N}$ in the sediment pool, 7 d and 14 d after rewetting, compared to the control with the absence of living *Hydrilla* (GLM, $p < 0.05$; Table 3). In contrast, the regrown *Cabomba* only significantly reduced the sediment ^{15}N pool at the rewetting period of 14 d, compared to other periods of rewetting. The regrown *Cabomba* significantly reduced the $\%^{15}\text{N}$ stored by PON, 3 d after rewetting, and the dissolved ^{15}N fraction, 7 d after rewetting, compared to the control with the absence of

living *Cabomba*. In contrast, the regrown *Hydrilla* did not significantly affect the ^{15}N distribution in the dissolved fraction or the PON during the entire rewetting period.

The percentage increase in biomass of regrown *Cabomba* and *Hydrilla* were not significantly different, except for 7 d after rewetting, when the percentage increase in regrown *Cabomba* biomass was significantly greater than *Hydrilla* ($F_{1,13} = 20.95$, $p < 0.05$, ANOVA; Fig. 3a).

Changes of Chl *a* in the water column after rewetting

The mean concentration of Chl *a* in the water column was significantly higher after 1 week of rewetting, compared to day 0 (GLM, $p < 0.05$, Fig. 3b,c). The dried then rewetted sediment treatment had significantly higher Chl *a* concentrations, compared to the constantly wet sediment treatment with the presence of living macrophytes after 2 weeks of rewetting. The *Cabomba* litter treatment had significantly higher Chl *a* concentrations, compared to the *Hydrilla* litter treatment after 2 weeks of rewetting, especially in the dried then rewetted sediment treatment.

Discussion

This study is the first, to our knowledge, to investigate the fate of N released from the litter of submerged macrophytes during a cycle of drying then rewetting. Our results showed that the fate of released N from desiccated macrophytes (macrophyte-derived N) after rewetting was impacted by (1) the sediment desiccation process (due to water level drawdown); (2) macrophyte species; and (3) the presence of living macrophytes (Fig. 4).

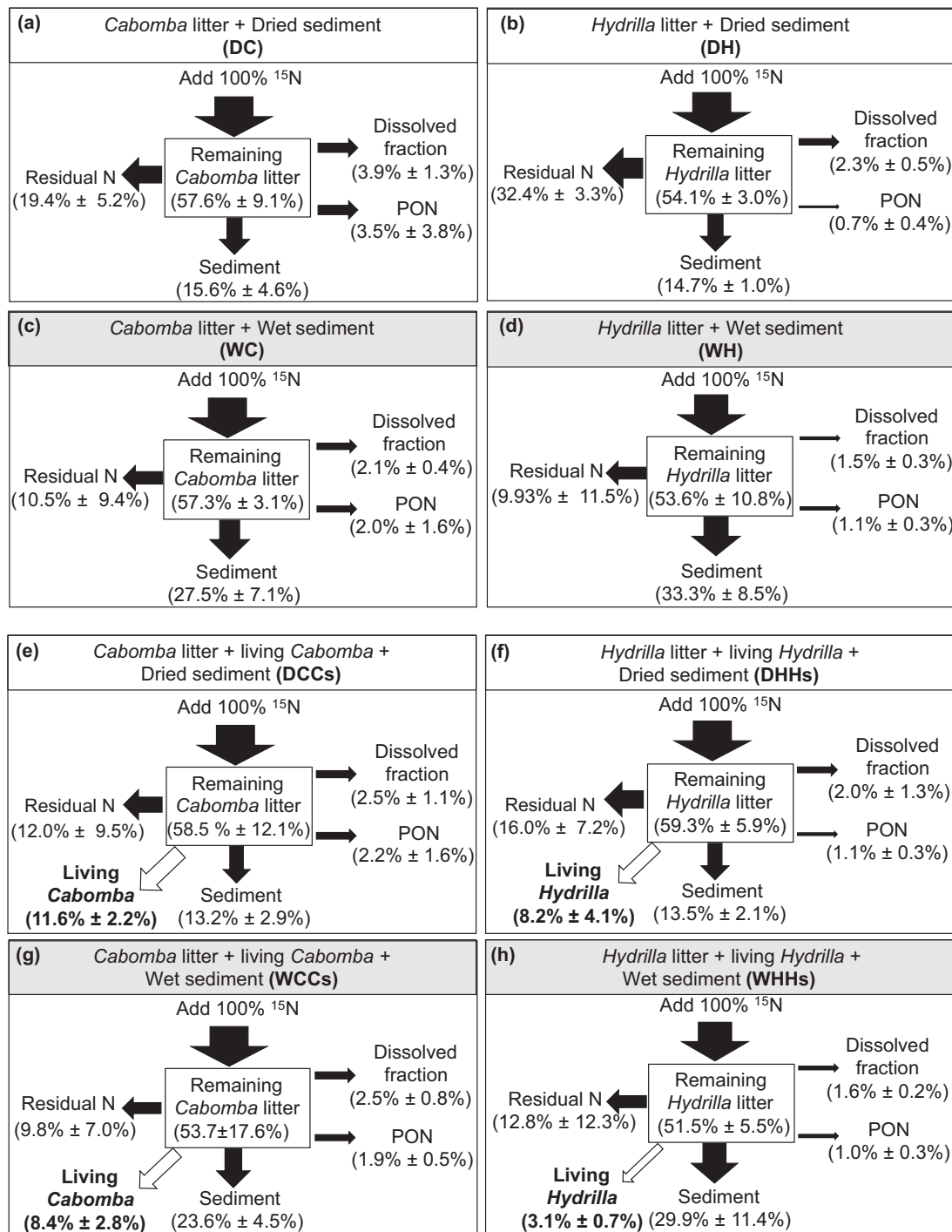


Fig. 2. The fate of ^{15}N from eight *Cabomba* and *Hydrilla* treatments, i.e. DC (a), DH (b), WC (c), WH (d), DCCs (e), DHHs (f), WCCs (g), WHHs (h), 28 d after rewetting, presenting as a standardized added ^{15}N percentage (% ^{15}N) relative to the initial input of ^{15}N in each treatment. The thickness of arrows presents the relative importance of each ^{15}N pool for macrophyte-derived ^{15}N .

Transformation of macrophyte-derived N between N pools after drying/rewetting

Our study showed that the ^{15}N released from macrophyte decomposition was rapidly transferred to the dissolved fraction of the water column, and quickly assimilated by PON, which is

likely dominated by phytoplankton (Del Giorgio and France 1996). The ^{15}N in these fractions was then gradually transferred into the sediment and, in the case of treatments with living macrophytes, incorporated into the biomass of regrown macrophytes. This time difference between phytoplankton and

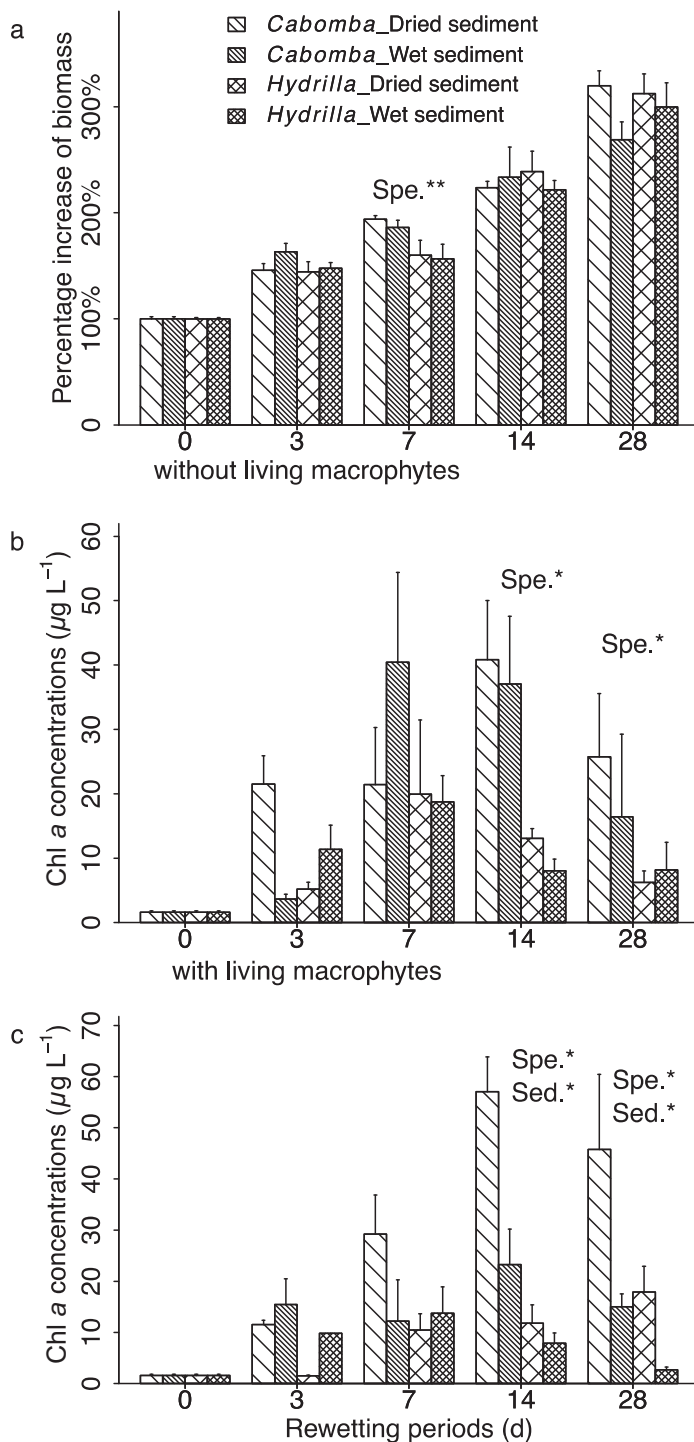


Fig. 3. The mean ($\pm$ SD) percentage increase in biomass (a) of regrown macrophytes in the four treatments containing living macrophytes (DCCs, WCCs, DHHs, and WHHs). The mean ($\pm$ SD) concentrations of water column Chl *a* in the treatments with the absence (b) and presence (c) of living macrophytes after rewetting. The Spe.* and Sed.* marked above bars refer to the significant differences between litter species (*Cabomba* and *Hydrilla*) and sediment history treatments (dried then rewetted and constantly wet) at $p < 0.05$ level, respectively, and ** indicates significant differences at $p < 0.01$ level.

regrown macrophytes for ^{15}N accumulation indicates that regrown macrophytes had a slower N uptake rate than phytoplankton in the water column. This rapid ^{15}N assimilation of phytoplankton also coincided with higher water column Chl *a* concentrations. Phytoplankton are capable of rapid N uptake with dissolved N turnover rates from minutes to hours (Lehman 1980; Glibert and Goldman 1981). Therefore, our results indicate that even though sediments are a long-term store of much of the N lost from macrophyte decomposition, the short-term (approximately the first week in our study) N flushed into the water column upon rewetting might become an important trigger for phytoplankton blooms.

Sediment desiccation and rewetting also have impacts on nutrient availability for phytoplankton in the water column. Previous studies have demonstrated that a N flush from dried sediment into the water column could occur upon rewetting. This N flush is mainly due to the increased mineralization of organic matter in the previously dried sediment after rewetting (known as “Birch effect”; Birch 1958; Qiu and McComb 1996). However, our study showed that the sediment desiccation can also cause a N flush from decayed macrophytes into the water column (Fig. 4a,b), compared to constantly wet conditions. Sediment desiccation in our study significantly increased the percentage of macrophyte-derived ^{15}N remaining in the dissolved fraction of the water column and transferred into regrown macrophytes, compared to the constantly wet conditions. In contrast, a higher proportion of macrophyte-derived ^{15}N was stored into the sediment when desiccation did not occur. The macrophyte-derived N remained in the water column, rather than stored in the sediment, is more likely to cause severe water quality deterioration in aquatic ecosystems, such as promoting phytoplankton blooms.

There are four possible reasons for this difference between different sediment desiccation history treatments. First, the increased mineral N content in the dried then rewetted sediment might slow down the ^{15}N diffusion from the water column to the sediment, which in turn increases the N diffusion from the latter to the former, due to a steeper concentration gradient at the sediment-water interface. Second, the sediment bulk density in our mesocosm increased, at least, 30–40% after complete desiccation. The compaction of sediment after desiccation might also result in a slower ^{15}N diffusion from the water column into the previously dried sediment (Barko et al. 1986). Third, the complete desiccation (soil moisture content 1.1%) in our study is also likely to reduce the microbial activities in the dried then rewetted sediment, resulting in less ^{15}N being processed by microbes into the previously dried sediment. Additionally, the constantly wet treatments could have more benthic algae growing on the surface of the sediment compared with the previously dried treatment. This could further increase the transportation of ^{15}N into the sediment pool.

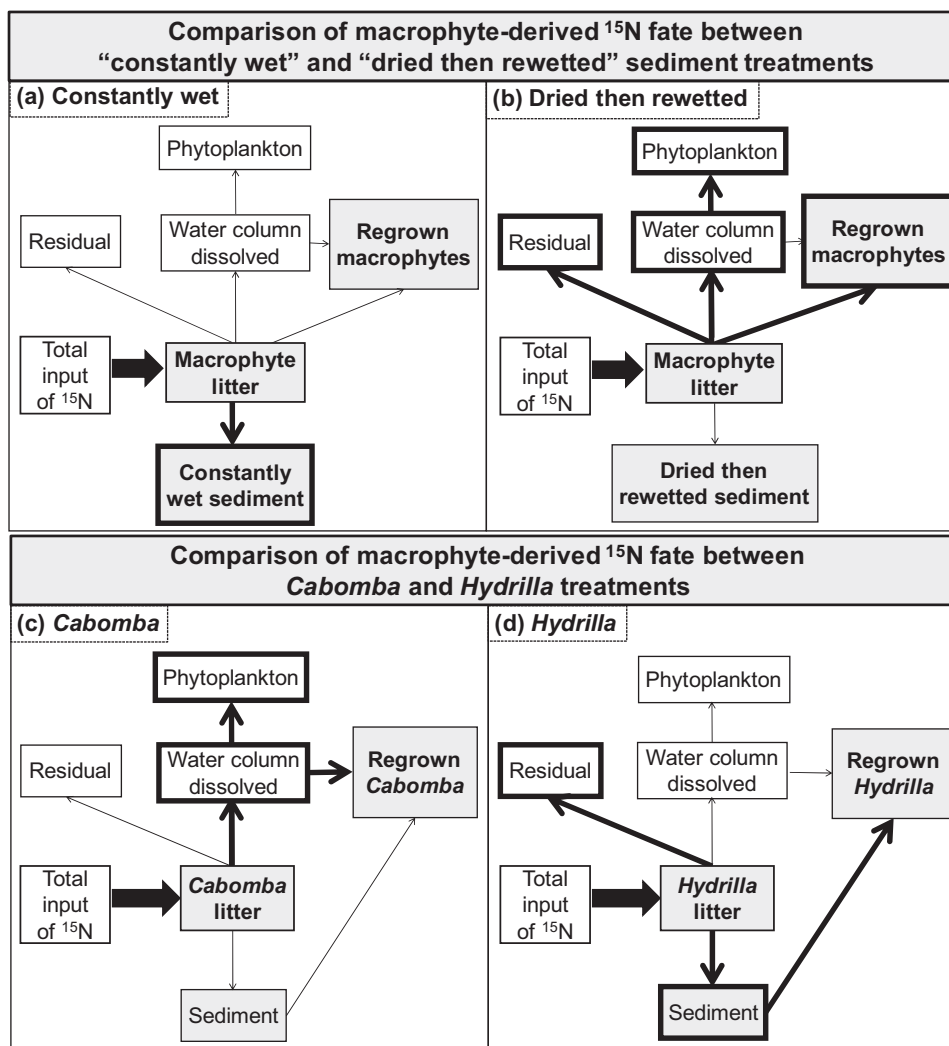


Fig. 4. Synthesis of experimental findings highlighting the comparison of the fate of macrophyte-derived ^{15}N between constantly wet (a) and dried then rewetted sediment (b) treatments and between *Cabomba* (c) and *Hydrilla* (d) treatments. The rectangle refers to different ^{15}N pools in the mesocosm. The shaded rectangles refer to the three main treatments in our study, i.e., T1: species differences in the litter, T2: sediment desiccation history, and T3: the presence of living macrophytes. The direction of arrows showed the ^{15}N flow from ^{15}N -labeled macrophyte litter to other N pools. The thickness of arrow presented the relative importance of each N pool compared between the constantly wet (a) and dried then rewetted sediment (b) treatments and between *Cabomba* (c) and *Hydrilla* (d) treatments.

Comparison of species differences in the litter on fate of macrophyte-derived N

Previous decomposition studies comparing macrophyte species typically compared the N release from the equivalent biomass between species (e.g., Battle and Mihuc 2000; Chimney and Pietro 2006; Lan et al. 2012). However, our study was able to compare the fate of released N relative to the total N content of the two species, using data from the ^{15}N -labeled macrophyte litter. Our standardized results showed that if *Cabomba* and *Hydrilla* having the same amount of ^{15}N in their biomass, significantly more proportion of the ^{15}N released from *Cabomba* litter was transferred to the dissolved fraction of the water column and assimilated by phytoplankton, compared to the *Hydrilla* litter (Fig. 4c,d). Moreover,

Cabomba litter had 1.6 times the TN content of *Hydrilla* litter in our study, indicating that a lower biomass of *Cabomba* litter (70% of equivalent *Hydrilla* biomass) can release the same amount of N as *Hydrilla* litter.

The higher percentage of released N remaining in the water column for the *Cabomba* litter treatment, compared to the *Hydrilla* litter in our study, is likely due to a faster decomposition rate for the *Cabomba* litter. We concluded this from the fact that a greater TN and biomass loss was measured in *Cabomba* litter than in *Hydrilla* litter after the same period of rewetting. *Cabomba* litter also had a significantly lower C : N ratio compared with *Hydrilla* litter, indicating a faster net decomposition rate and faster N release rate for *Cabomba* litter (Geurts et al. 2010).

The *Cabomba* treatment also resulted in a higher ^{15}N storage in the phytoplankton, as well as higher TDN and TDP concentrations, and lower DO concentrations in the water column, compared to the *Hydrilla* treatment after rewetting. This indicates that the invasive *Cabomba* is more likely to cause more severe water quality deterioration after drying then rewetting, compared to native *Hydrilla*.

The effect of regrowth of submerged macrophytes on macrophyte-derived N

Our study also demonstrated the effect of macrophyte regrowth on redistributing macrophyte-derived N within different N pools. The regrown macrophytes were the second largest ^{15}N pool (smaller than the sediment pool) for the released N from macrophyte decomposition. The ^{15}N assimilated by regrown *Cabomba* and *Hydrilla* were $30\% \pm 7\%$ and $20\% \pm 5\%$ of total released ^{15}N in dried then rewetted treatments, and $18\% \pm 10\%$ and $6\% \pm 3\%$ of total released ^{15}N in constantly wet treatments, 28 d after rewetting. The regrowth of *Hydrilla* also significantly reduced the sediment ^{15}N , while regrown *Cabomba* significantly reduced the ^{15}N in the water column and PON (Fig. 4c,d). This indicates that regrown *Hydrilla* might assimilate more proportion of assimilated N from the sediment than from the water column, compared with regrown *Cabomba*. However, both regrown *Cabomba* and *Hydrilla* significantly reduced water column TDN concentrations 28 d after rewetting, by which time the plant biomass had reached approximately 4.5 kg m^{-3} in the mesocosm. This indicates a species- and biomass-dependent effect of regrown submerged macrophytes on reducing water column N. Therefore, maintaining a certain amount of submerged macrophytes could be a key factor in alleviating the nutrient increase thus phytoplankton growth in the water column during WLFs.

Potential N removal from the system by desiccation and macrophyte regeneration

The mean recovery of ^{15}N in our study ($90\% \pm 12\%$) was comparable to other plant-derived ^{15}N tracing studies in forest or farmland settings (Müller and Sundman 1988; Zeller et al. 2000, 2001), which were ranged from 89% to 102%. Sediment desiccation in our study reduced the ^{15}N recovery, compared to the constantly wet sediment treatment and/or the dried then rewetted sediment treatment with living macrophytes. One possible explanation for this difference is that a higher proportion of N from macrophyte decomposition in the dried then rewetted treatment was converted to gaseous N, and removed from the system by denitrification. Increased denitrification after drying then rewetting, compared with constantly wet conditions, has also been determined in several previous studies (e.g., Smith and Parsons 1985; Groffman and Tiedje 1988; Fromin et al. 2010). This increased denitrification is likely due to increased carbon and N mineralization during the drying and rewetting cycle, resulting in the increased coupled nitrification-denitrification. Specifically, the carbon and

N (e.g., NH_4^+) released from drying then rewetting can provide nitrifiers the energy and substrates that required for nitrification, which oxidized NH_4^+ to NO_3^- (Stanley and Boulton 1995; Qiu and McComb 1996; Baldwin et al. 2000). This increased NO_3^- concentrations from nitrification, in turn, can provide substrates and electron acceptors thus promoting denitrification (NO_3^- to N_2 or N_2O) after rewetting, especially when anaerobic conditions occur after drying then rewetting. This is because the faster activation of denitrifying enzymes by oxygen depletion resulted from the flush of microbial respiration and macrophytes decomposition (Smith and Parsons 1985; Kern et al. 1996). However, when submerged macrophytes regrow after rewetting they may compete with nitrifiers for the available mineral N (Bodelier et al. 1998), which may limit subsequent nitrification-denitrification (Baldwin and Mitchell 2000; Cavanaugh et al. 2006).

In summary, our study indicates that the water level drawdown followed by rewetting can cause a flush of macrophyte-derived N transferring into the water column and assimilated by phytoplankton, increasing impacts on water quality, compared to constantly wet conditions. Water level drawdown followed by rewetting is also an important trigger for macrophytes loss and subsequent decomposition. The invasive species *Cabomba* can cause more serious water quality deterioration (higher TDN and TDP, higher Chl *a*, and lower DO concentrations) after rewetting, compared to the native *Hydrilla*, as a result of the higher TN content and faster decomposition rate of this litter. The regrowth of submerged macrophytes is able to reduce the N content in the sediment and/or in the water column pool, playing a positive role in counteracting N release from macrophyte litter. However, the scale of this effect was species- and biomass-dependent. These findings add to our understanding of N dynamics in littoral macrophytes, and key factors affecting the macrophyte-derived N fate during WLFs in shallow aquatic ecosystems.

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Conflict of Interest

None declared.

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