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Heat Waves Alter Macrophyte-Derived Detrital Nutrients Release under Future Climate Warming Scenarios

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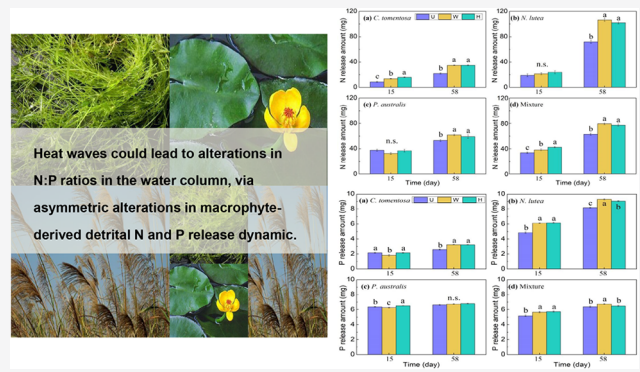
ABSTRACT: In addition to a rise in global air and water mean temperatures, extreme climate events such as heat waves are increasing in frequency, intensity, and duration in many regions of the globe. Developing a mechanistic understanding of the impacts of heat waves on key ecosystem processes and how they differ from just an increase in mean temperatures is therefore of utmost importance for adaptive management against effects of global change. However, little is known about the impact of extreme events on freshwater ecosystem processes, particularly the decomposition of macrophyte detritus. We performed a mesocosm experiment to evaluate the impact of warming and heat waves on macrophyte detrital decomposition, applied as a fixed increment (+4 °C) above ambient and a fluctuating treatment with similar energy input, ranging from 0 to 6 °C above ambient (i.e., simulating heat waves). We showed that both warming and heat waves significantly accelerate dry mass loss of the detritus and carbon (C) release but found no significant differences between the two heated treatments on the effects on detritus dry mass loss and C release amount. This suggests that moderate warming indirectly enhanced macrophyte detritus dry mass loss and C release mainly by the amount of energy input rather than by the way in which warming was provided (i.e., by a fixed increment or in heat waves). However, we found significantly different amounts of nitrogen (N) and phosphorus (P) released between the two warming treatments, and there was an asymmetric response of N and P release patterns to the two warming treatments, possibly due to species-specific responses of decomposers to short-term temperature fluctuations and litter quality. Our results conclude that future climate scenarios can significantly accelerate organic matter decomposition and C, N, and P release from decaying macrophytes, and more importantly, there are asymmetric alterations in macrophyte-derived detrital N and P release dynamic. Therefore, future climate change scenarios could lead to alterations in N/P ratios in the water column via macrophyte decomposition processes and ultimately affect the structure and function of aquatic ecosystems, especially in the plankton community.



1. INTRODUCTION

Ecosystems are experiencing not only gradual shifts in mean climate conditions but also dramatic changes in climate variability and increased prevalence of extreme climatic events.[1] Extreme climatic events such as heat waves are predicted to occur more frequently, become more intense, and last longer.[2−5] Freshwater ecosystems, such as shallow lakes and ponds, are particularly sensitive to heat waves as their average water temperature will increase more quickly than that in deeper water bodies as a result of their close link to air temperature.[6] Shifts in the mean temperature but also of the variability of environmental factors have been shown to modify key biological processes and alter structure and functioning of ecosystems.[7−10]

Aquatic macrophytes are recognized for their ecosystem services in shallow freshwater ecosystems.[11,12] When they die and decompose, vast concentrations of nutrients are released from plant litter, resulting in seasonal deterioration of the water quality.[13] In aquatic ecosystems, macrophyte-derived detritus decomposition is influenced not only by internal factors, such as initial litter quality, but also by external environmental factors such as water temperature,[14−17] composition of the decomposer community,[14,18] and nutrient availability in the water column,[19] as well as in the sediment.[20] Among them, temperature is one of the most critical factors controlling decomposition processes.[14,21] Previous studies have corroborated that higher water temperature significantly

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speeds up the decomposition rate and reduces organic carbon burial in shallow lakes, both directly, by promoting leaching of soluble compounds,[22] and indirectly, by affecting the aquatic decomposer dynamics and interactions between fungi and bacteria[14,15,18,21,23,24] and enhancing enzyme activities.[25,26] These impacts derive from a combination of changes in average climate conditions and extreme climate events. However, to date, most studies on the effects of warming have focused on the effects of increased mean temperatures on litter decomposition.[15,17,23,25,27] Our understanding of how an increase in mean temperature affects organic matter decomposition processes is growing,[21,23,28−31] but we still know relatively little about how those effects will differ in a climate scenario with increased variability in temperature, including extreme heat events, rather than fixed warming alone. Heat waves may potentially have a more pronounced impact on ecosystems than changes in mean temperatures alone.[4,5] Recent findings suggest that short-term temperature fluctuations may have considerable effects on litter decomposition, especially when they affect processes governed by microorganisms or microbial communities that rapidly respond to temperature changes.[14,24] Although these findings highlight the importance of considering heat events when assessing consequences of climate warming on detritus decomposition, the effects of heat waves on macrophyte-derived detritus decomposition are largely unknown.

In addition to temperature, litter quality (i.e., the contents of carbon, nitrogen, phosphorus, cellulose, and lignin) is also an important factor affecting decomposition processes in freshwater systems.[20,32−34] Organic matter quality and quantity, via litter inputs, have been found to control microbial decomposers. Different species of macrophytes vary significantly in terms of their physical structure, chemical composition, particle size, and ability to be colonized by microbes during decomposition.[18] Also, the decomposition of a single macrophyte species may not mirror the nutrient cycling in aquatic ecosystems since several species co-occur and decay simultaneously in natural ecosystems.[35] Mixed litter can create diverse decomposition habitats and increase resource availability, thus supporting different decomposer groups and causing complex cascade effects that can facilitate nutrient transfer and chemical inhibition during decomposition.[36] Previous findings regarding how litter mixing influences decomposition and nutrient dynamics have been contradictory, showing antagonistic, synergistic, or no effects of mixing.[37,38] The interactions of heat waves and litter quality may induce different litter-mixing effects. It is therefore important to advance our understanding of potential interactions between future climate scenarios and organic matter quality in driving the decomposition process.

The decomposition of aquatic macrophytes detritus is an essential ecological process influencing carbon (C), nutrient cycling, and energy flows in aquatic ecosystems.[32,39] Climate change will not only shift environmental means but will also increase the intensity of extreme events, exerting additional stress on ecosystems.[10] Understanding and distinguishing the effects of an increase in mean temperature and heat wave on macrophyte detritus decomposition are crucial for gaining a fundamental understanding of nutrient cycling in freshwater ecosystem. Therefore, we conducted a mesocosm experiment to assess the responses of different climate scenarios on the decomposition of three common macrophytes, *Chara tomentosa*, *Phragmites australis*, and *Nuphar lutea*, representing different life-forms, and their mixture. In particular, our study design evaluated how the effects of warming variability, including extreme heat events, differed from a climate scenario with a fixed increment warming on macrophyte-derived detritus decomposition. We hypothesized that increased warming variability, with increased frequency of heat waves, affects macrophyte decomposition processes differently when compared to a fixed increment in temperature. We also predicted a stronger positive effect of fluctuating warming on the detritus decomposition rate and nutrient release than at an elevated constant mean temperature because short-term warming fluctuations may mainly favor and process organisms that respond rapidly to temperature changes, such as bacteria and fungi.[14,25]

2. MATERIAL AND METHODS

2.1. Experimental Setup. An outdoor mesocosm experiment, consisting of 24 insulated polyethylene enclosures (0.7 m in diameter, 1 m in height), was conducted between June 26 and August 22, 2014, at Lund University (N55°42′46″, E13°12′26″). The enclosures were randomly distributed on a flat area and filled with 400 L of unfiltered lake water collected from the eutrophic Lake Krankesjön (N55°42′, E13°27′), a shallow lake located in Southern Sweden. For a more thorough lake description, consider Hansson et al.[11]

Our study consisted of three temperature treatments (each replicated eight times): controls, mimicking the current climate state in a temperate shallow lake in southern Sweden (hereafter named U treatment: unheated treatment); a treatment where the temperature followed the ambient daily and seasonal variations, but at a 4 °C higher level (hereafter named W treatment: warmed); and finally, a treatment with a preprogrammed fluctuating temperature, ranging from 0 to 8 °C above ambient conditions (hereafter named H treatment: heat waves), mimicking the predicted future climate scenario of more frequent and intense temperature variations.[4] The frequency and amplitude of the heat waves were based on model predictions from IPCC (2013) and the Swedish Meteorological and Hydrological Institute (SMHI) for a climate scenario about 75 years into the future. Both W and H treatments had the same long-term mean temperature increase of +4 °C, so they only differed in how warming fluctuated. The increase in temperature in the W and H treatments was achieved by using a computer-controlled temperature system that regulated the elevated temperature in the treatments based on the mean temperature in the unheated mesocosms.[7,9,40] The temperature of each mesocosm was measured every 10 s using automatic thermal sensors (National Semiconductor, LM335AZ, precision temperature sensor), and if the temperature in any of the W and H mesocosms differed more than 0.2 °C from the desired temperature, an aquarium heater (Jäger 150 W, EHEIM GmbH & Co, Stuttgart, Germany) of that specific mesocosm was turned on or off until the desired temperature was reestablished. The heater automatically turned off if the water temperatures increased above 30 °C. All mesocosms were kept open during the experiment, allowing rainfall to enter. Water levels were maintained by the weekly addition of deionized water to ensure all 24 enclosures had the same level. Deionized water was used instead of tap water to avoid elevated salinity in the mesocosms. To maintain productivity, all mesocosms received the same amount of nutrients during the experiment by biweekly addition of 1 mL of commercial plant nutrients

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(Blomstra växtnäring, Cederroth, Upplands Väsby, Sweden; 50.1 g/L total nitrogen, and 10.0 g/L total phosphorous).

2.2. Experimental Materials and Litter Bags. Three representative well-grown macrophyte species for the region, *Chara tomentosa*, *Nuphar lutea*, and *Phragmites australis*, were collected from different sites around the same lake as the water was taken from. In this study, we used the entire plants of *C. tomentosa*, leaves and petioles of *N. lutea*, and stems and leaves of *P. australis* as experimental materials. The collected plant materials were washed with water to exclude any unwanted material and then oven-dried at 60 °C to constant dry weight. 600 g of the dried plant material from each species was then cut into 5 mm long pieces. Then, 4 g of litter of each macrophyte or three species mixture combined at a dry weight ratio of 1:1:1 was placed into a nylon mesh bag (7 cm × 7 cm; 250 μm in mesh size), which were sewn shut using nylon thread. A total of 192 litter bags were produced, that is, four species (three macrophytes and their mixture) × three temperature treatments × eight replicates. Four litter bags (three single species and one mixture) were randomly bound together in a cluster using a plastic clip, and 48 clusters in total were prepared for the decomposition experiments. On June 26, 2014, two clusters attached ropes were randomly placed onto the bottom of each enclosure.

2.3. Sampling and Chemical Analyses. The first litter bag cluster was taken out from each mesocosm in order to measure the concentrations of carbon (C), nitrogen (N), phosphorus (P), and the remaining dry weight of the three macrophytes and their mixture after 15 days, and the second litter bag cluster was taken out after 58 days, i.e., at the end of the experiment. The remaining material in each litter bag was transferred into paper bags and oven-dried to constant weight at 60 °C. Finally, the remaining material from each bag was weighed and ground to fine powders with a mortar for chemical analyses.

The total C and N concentrations of the initial litter samples (before the experiment started) and the remaining material (at days 15 and 58) were determined from 5−6 mg of homogeneously ground material of the three macrophytes and the mixture using an Elemental Analyzer (NA2500, Carlo Erba Reagenti, Milan, Italy). The total P content was measured using a colorimeter, an AutoAnalyzer (Bran+Luebbe GmbH, Inc., Germany), after sulfuric acid/hydrogen peroxide digest and the ammonium molybdate ascorbic acid method.[41]

2.4. Data Analysis. One-way analysis of variance (ANOVA) was used to analyze differences in the initial C, N, and P contents and their stoichiometric ratio among the different macrophyte species and their mixture. A mixed-effects ANOVA was used to examine the effects of the species identity (each species and the mixture; in total four levels), temperature treatments, sampling date, and their interaction on the remaining biomass and the amounts of C, N, and P released (initial value minus remaining value in the plant sample at each sampling occasion). The species identities were the random effect, and temperature treatments were the main effect (fixed). As we performed the destructive sampling, we could not use repeated measures ANOVA. The sampling date was considered a random factor. The model was expressed as

$$V_{ijkn} = \mu + S_i + D_k + T_j \times S_i + T_j \times D_k + S_i \times D_k + \varepsilon$$

where V_{ijkn} represents the nth observation of variables under ith species identity (S, four levels), jth temperature treatment (T, three levels), kth sampling date (D, three levels), μ is the mean of corresponding variables, and ε is the unobserved error component. The residuals followed the normal distribution through the histogram and P−P (probability−probability) plots in residuals analysis. Duncan post hoc analyses were performed to determine the significant differences between species or treatments.

A structural equation model (SEM) was applied to quantify the relative contributions of the temperature treatment and the initial nutrient contents of the macrophytes and their mixtures on the comprehensive decomposition process (as shown by the overall dry mass loss and amounts of C, N, and P released). Data used for the initial nutrient contents were the PC_1 from the principal component analysis (PCA) on the C, N, and P contents of the three macrophytes and their mixtures, and data used for the comprehensive decomposition were the PC_1 from the PCA on accumulative dry mass loss and the amounts of C, N, and P released at 15 and 58 days. The two PC_1 explained 96.4 and 75.2% of the total variance, respectively. A maximum likelihood estimation method was used to fit the SEM. The adequate model goodness-of-fit was evaluated by Chi-squared tests, goodness of fit index (GFI), comparative fit index (CFI), and root mean square error of approximation (RMSEA).

All the statistical analyses except for SEM were performed with R (R Core Team 2013). The PCA were performed using the R-Vegan package.[42] The SEM was constructed using AMOS 22.0 (IBM, SPSS, Armonk, NY, USA). All significant differences were set at a level of α = 0.05, unless otherwise stated.

3. RESULTS

3.1. Background Variables. The highest recorded water temperatures in U, W, and H treatments reached 25.7, 29.3, and 30.2 °C, respectively (Figure 1). The difference in average

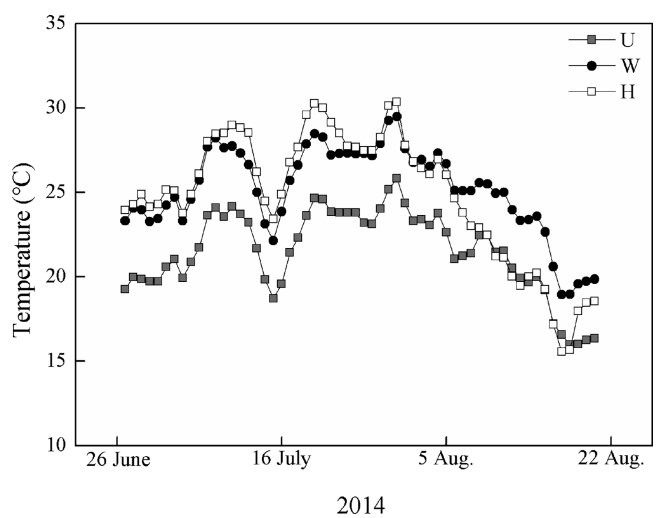

Figure 1. Mean daily temperature trajectories (°C) of mesocosms subject to three temperature scenarios from June 26 to August 22, 2014 (U: unheated treatment, W: a fixed increment warming treatment, and H: heat wave treatment).

temperatures between the U and the H treatments ranged from +0 to 6 °C. During the experiment, the temperature in the H-mesocosm was higher than that in the W-mesocosm during 16 days and lower during 18 days. However, the long-term mean temperature recorded in the H-mesocosm was very close to the W-mesocosm, and the mean temperatures in W and H

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Table 1. Initial Nutrient Characteristics (Mean ± SD, $n = 4$) of the Detritus of Three Tested Macrophytes and Their Mixtures[1]

	C%	N%	P%	C/N	C/P	N/P
Chara tomentosa	21.09 ± 0.49 d	1.01 ± 0.01 c	0.09 ± 0.01 c	20.84 ± 0.34 a	248.88 ± 16.42 a	11.94 ± 0.77 a
Nuphar lutea	41.61 ± 0.39 b	3.08 ± 0.11 a	0.25 ± 0.01 a	13.55 ± 0.34 c	165.93 ± 3.59 b	12.26 ± 0.22 a
Phragmites australis	42.81 ± 0.05 a	2.51 ± 0.12 b	0.19 ± 0.00 b	17.18 ± 0.88 b	221.68 ± 4.46 a	12.96 ± 0.42 a
mixture	35.74 ± 0.16 c	2.37 ± 0.03 b	0.19 ± 0.00 b	15.07 ± 0.18 c	185.19 ± 4.03 b	12.29 ± 0.16 a
F value	958.64	116.82	163.88	38.65	17.25	0.87
P value	<0.001	<0.001	<0.001	<0.001	<0.001	n.s.

[a]The results from one-way ANOVA are shown, and significant differences between means within columns evaluated at $P < 0.05$ are indicated by different letters. n.s., nonsignificant ($P > 0.05$).

Table 2. Results from an ANOVA Testing the Effects of Macrophyte Species, Temperature Treatment, Sampling Date, and Their Interaction on Accumulative Dry Mass Loss, and the Accumulative Amounts of C, N, and P Released[a]

	dry mass loss			C release amount			N release amount			P release amount		
effects	df	*F* value	*P* value	df	*F* value	*P* value	df	*F* value	*P* value	df	*F* value	*P* value
macrophyte species (S)	3	85.44	<0.001	3	502.23	<0.001	3	79.50	<0.001	3	359.94	<0.001
temperature treatment (T)	2	20.41	<0.001	2	88.06	<0.001	2	13.72	0.001	2	7.76	0.007
sampling date (D)	2	1974.33	<0.001	2	8657.73	<0.001	2	901.76	<0.001	2	2655.47	<0.001
$S \times T$	6	0.99	n.s.	6	1.78	n.s.	6	1.40	n.s.	6	2.15	n.s.
$S \times D$	6	24.84	<0.001	6	169.94	<0.001	6	53.16	<0.001	6	112.53	<0.001
$T \times D$	4	5.97	0.007	4	25.17	<0.001	4	8.68	0.002	4	2.39	n.s.

[a]n.s., nonsignificant ($P > 0.05$).

Table 3. Percentages (Mean ± SD, $n = 8$) of the Biomass Loss and Amounts of C, N, and P Released from the Detritus of Three Macrophytes and Their Mixtures at the End of the Experiment of Their Initial Amounts (U: Unheated Treatment, W: Fixed Increment Warming Treatment, and H: Heat Wave Treatment)[a]

macrophyte species	experimental treatment	biomass loss (%)	C (%)	N (%)	P (%)
Chara tomentosa	U	68.61 ± 1.15 b	73.86 ± 1.07 b	53.85 ± 2.30 b	75.54 ± 2.03 b
	W	92.68 ± 0.76 a	92.57 ± 0.58 a	86.50 ± 1.18 a	94.50 ± 0.70 a
	H	92.62 ± 0.84 a	93.21 ± 0.65 a	86.80 ± 1.87 a	94.12 ± 0.66 a
	mean ($n = 24$)	84.64 ± 2.42 A	86.54 ± 1.92 A	75.72 ± 3.38 A	88.05 ± 1.98 A
Nuphar lutea	U	76.05 ± 0.50b	71.45 ± 0.62b	58.42 ± 1.90b	81.42 ± 0.66c
	W	86.50 ± 1.42 a	83.85 ± 1.81 a	86.60 ± 2.28 a	92.65 ± 0.84 a
	H	84.53 ± 0.92 a	81.19 ± 1.18 a	82.94 ± 1.62 a	90.19 ± 0.63 b
	mean ($n = 24$)	82.36 ± 1.10 A	78.83 ± 1.32 B	75.99 ± 2.82 A	88.09 ± 1.08 A
Phragmites australis	U	46.20 ± 0.53 b	42.59 ± 0.62 b	52.85 ± 1.72 b	85.77 ± 0.93 a
	W	53.44 ± 1.15 a	49.62 ± 1.26 a	61.51 ± 1.23 a	87.15 ± 0.70 a
	H	52.54 ± 1.18 a	48.16 ± 1.22 a	58.92 ± 2.48 a	88.07 ± 0.64 a
	mean ($n = 24$)	50.73 ± 0.87 B	46.79 ± 0.87 C	57.76 ± 1.28 B	87.00 ± 0.47 A
mixture	U	76.33 ± 0.55 b	69.25 ± 0.73 b	66.18 ± 1.82 b	82.64 ± 1.08 b
	W	84.90 ± 0.80 a	80.42 ± 0.99 a	83.60 ± 1.50 a	87.36 ± 1.00 a
	H	84.09 ± 1.07 a	79.37 ± 1.36 a	81.45 ± 1.78 a	83.88 ± 1.22 b
	mean ($n = 24$)	81.77 ± 0.93 A	76.35 ± 1.20 B	77.08 ± 1.87 A	84.62 ± 0.74 A

[a]Significant differences between means within columns evaluated at $P < 0.05$ are indicated by different letters, and capital letters and lowercase letters indicated different species and different treatments of the same species, respectively.

treatments during the experiment were 25.1 and 24.7 °C, respectively (Figure 1). The P concentrations were generally below 50 μg/L, which was below the detection limit for our analyses.

The initial C%, N%, P%, C/N, and C/P differed significantly among the three species and their mixture, although the difference in the initial N/P ratio was not significant (Table 1). The floating-leaved macrophyte *N. lutea* exhibited the highest N% and P%, and the submerged macrophyte *C. tomentosa* had the lowest N% and P%. The initial N and P contents in *N. lutea* were three times higher than those in *C. tomentosa*. However, there was no discernible difference in the initial N and P concentrations between the emergent macrophyte *P. australis* and the mixture. Furthermore, the C/N and C/P ratios of *N. lutea* and mixture were significantly lower than those of *C. tomentosa* and *P. australis* (Table 1).

3.2. Detritus Dry Mass Loss. The dry mass loss showed significant differences among the three macrophyte species and the mixture, as well as among the three temperature treatments. However, the interactive effect of species and temperature treatment on detritus dry mass loss was not significant (Table 2).

P. australis showed significantly lower dry mass loss than *C. tomentosa*, *N. lutea*, and the mixture, whereas there was no significant difference in the dry mass loss among *C. tomentosa*, *N. lutea*, and mixture (Table 3). At the end of the experiment, *C. tomentosa*, *N. lutea*, *P. australis*, and mixture bags in the U treatment decreased, on average, by 68.6, 76.1, 46.2, and 76.3%

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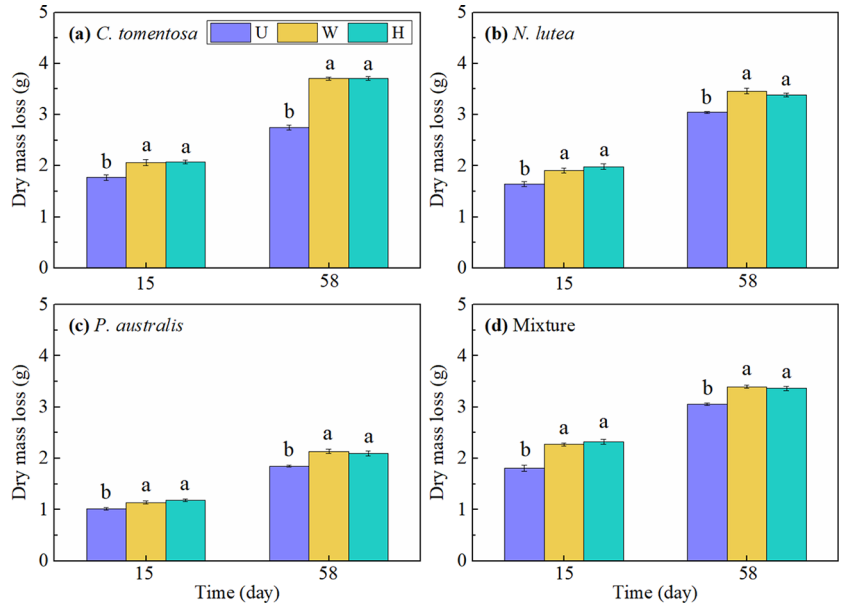

Figure 2. Accumulated dry biomass losses (mean ± SD, n = 8) of three macrophytes and the mixtures at different temperature scenarios at 15 and 58 days (U: unheated treatment, W: a fixed increment warming treatment, and H: heat wave treatment. Different letters indicate significant differences (P < 0.05) between the treatments as detected in Duncan post hoc analyses for a particular day).

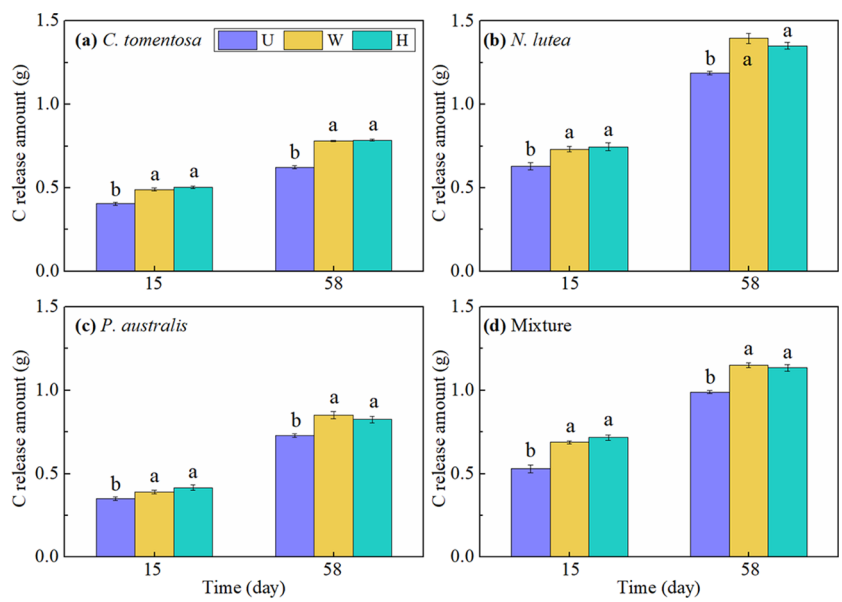

Figure 3. Accumulated amounts of C released (mean ± SD, n = 8) from the detritus of three macrophytes and the mixtures at different temperature scenarios at 15 and 58 days (U: unheated treatment, W: a fixed increment warming treatment, and H: heat wave treatment. Different letters indicate significant differences (P < 0.05) between the treatments as detected in Duncan post hoc analyses for a particular day).

of their initial dry mass, respectively. *C. tomentosa*, *N. lutea*, *P. australis*, and the mixture had lost 92.7, 86.5, 53.4, and 84.9% of their initial dry mass, respectively, in the W treatment, and the corresponding losses in the H treatment were 92.6, 84.5, 52.5, and 84.1%, respectively (Table 3).

For the temperature treatments, the three macrophyte species and their mixture showed similar response patterns in dry mass loss. The four litter bag types all showed higher dry mass loss in the W and H treatments than in the U treatment throughout the experiment (Table 3). However, no significant differences were found in dry mass loss of the three macrophytes and their mixture between the W and H treatments at the beginning and end of the experimental period (Figure 2).

3.3. Detritus C, N, and P Release Dynamics. Both macrophyte species and temperature treatment alone significantly influenced the accumulated amounts of C, N, and P released, whereas the interaction effects of species and temperature treatment on the accumulated amounts of C, N, and P released were not significant (Table 2). The differences were distinct with respect to C release among the three macrophyte species and their mixture. The highest C release was found in *C. tomentosa*, although nonsignificant differences were detected between *N. lutea* and the mixture (Table 3). However, no significant differences were detected in P release

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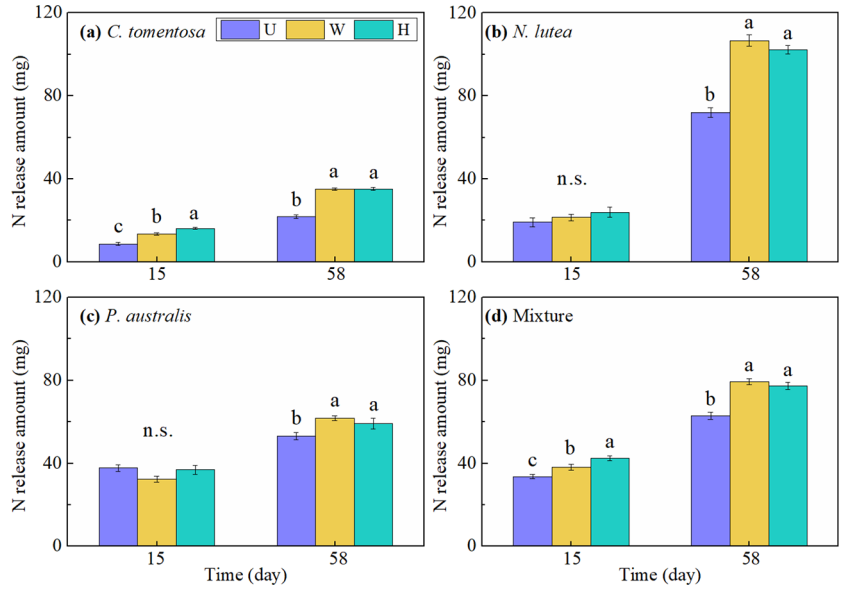

Figure 4. Accumulated amounts of N released (mean ± SD, n = 8) from the detritus of three macrophytes and the mixtures at different temperature scenarios at 15 and 58 days (U: unheated treatment, W: a fixed increment warming treatment, and H: heat wave treatment. Different letters indicate significant differences (P < 0.05) between the treatments as detected in Duncan post hoc analyses for a particular day. n.s.: P > 0.05).

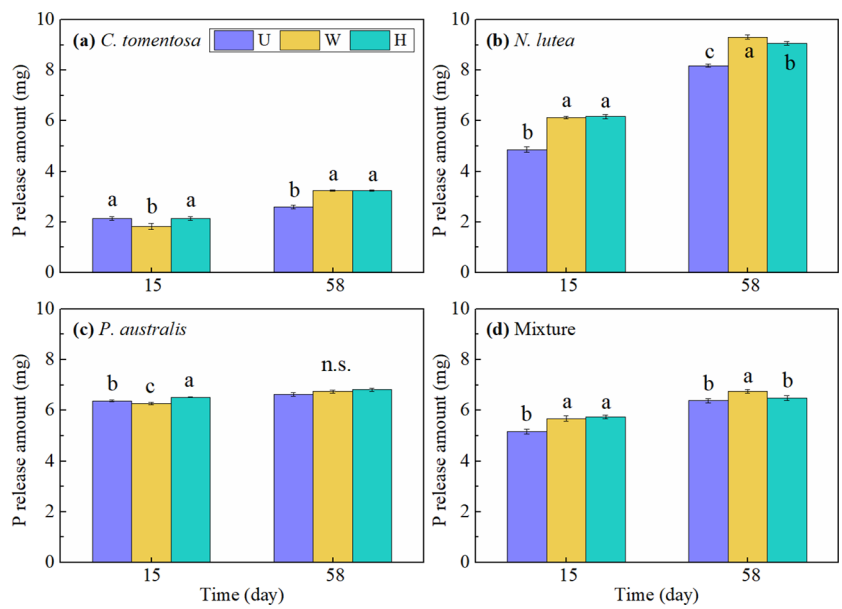

Figure 5. Accumulated amounts of P released (mean ± SD, n = 8) from the detritus of three macrophytes and the mixtures at different temperature scenarios at 15 and 58 days (U: unheated treatment, W: a fixed increment warming treatment, and H: heat wave treatment. Different letters indicate significant differences (P < 0.05) between the treatments as detected in Duncan post hoc analyses for a particular day. n.s.: P > 0.05).

among the three macrophyte species and their mixture or in N release among *C. tomentosa*, *N. lutea*, and the mixture (Table 3). During the experiment, *P. australis* released the lowest amounts of C and N among the three macrophytes and their mixture. At the end of the experiment, *C. tomentosa*, *N. lutea*, *P. australis*, and the mixture had released 73.9, 71.5, 42.6, and 69.3%, respectively, of their initial C amount in the U treatments. In the W treatments, the losses of C were 92.6, 83.9, 49.6, and 80.4%, respectively, and in the H treatments, losses were 93.2, 81.2, 48.2, and 79.4%, respectively. The amounts of N released in the U, W, and H treatments from *C. tomentosa* were 53.9, 86.5, and 86.8%, respectively, of the initial values; from *N. lutea*, the amounts were 58.4, 86.6, and 82.9%, respectively; from *P. australis*, the amounts were 52.9, 61.5, and 58.9%, respectively; and from the mixture, the amounts were 66.2, 83.6, and 81.5%, respectively. The mean proportions of P released of their initial values in the U, W, and H treatments from *C. tomentosa*, *N. lutea*, *P. australis*, and mixture were 88.1, 88.1, 87.0, and 84.6%, respectively (Table 3).

For different temperature treatments, the three macrophyte species and their mixtures displayed the same patterns in the C release amount during the experiment. The three macrophyte species and their mixtures all released more C in the W and H treatments than in the U treatment, while no detectable differences in C release were observed between the W and H treatments at either 15 or 58 days (Figure 3).

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The three macrophyte species and their mixtures also showed similar patterns in N release dynamics for the different temperature treatments. After 15 and 58 days, the three macrophytes and their mixture had a significantly higher cumulative N release in the W and H treatments than in the U treatment, except for the nonsignificant difference among the U, W, and H treatments for *N. lutea* and *P. australis* after 15 days. Interestingly, *C. tomentosa* and the mixture released significantly higher amounts of N in the H treatment than in W treatment after 15 days, while there was a nonsignificant difference in the amount N released from the three macrophytes and their mixture between the W and H treatments at 58 days (Figure 4).

In contrast to the C and N release patterns, P release dynamics of the three single species and their mixture responded differently to the temperature treatments. *C. tomentosa* detritus had released more P in U and H treatments than in the W treatment after 15 days and had released more P in W and H treatments than in the U treatment after 58 days (Figure 5). For the amount of P released from *P. australis* detritus, there were significant differences among the three temperature treatments at day 15 and nonsignificant differences at day 58 (Figure 5). *N. lutea* and the mixture displayed similar P release dynamics by showing significantly higher P release in the W and H treatments than in U treatment at both day 15 and day 58, except for the mixture in U and H treatments at day 58. Moreover, *N. lutea* and the mixture released more P in the W treatment than in the H treatment at day 58 (Figure 5).

3.4. Effect of Species and Temperature Treatment on Macrophyte Decomposition. Considering the accumulated dry mass loss and amounts of C, N, and P released together as the macrophyte decomposing process, plant species (i.e., initial C, N, and P contents) contributed more than temperature treatment to the macrophyte decomposition (Figure 6). The standardized path coefficients of the species and temperature treatment to the comprehensive decomposition were 0.261 and 0.196, respectively. The species and temperature treatment together explained 10.6% of the variations in the macrophyte decomposition.

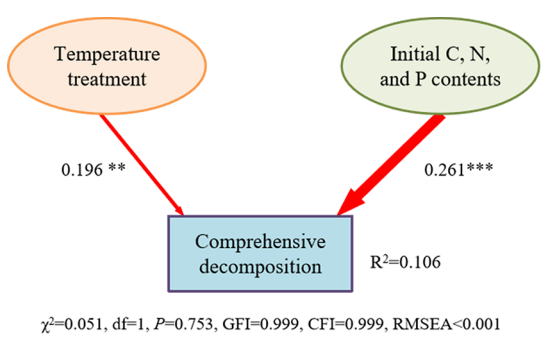

Figure 6. Structural equation model showing the contributions of the temperature treatment and initial C, N, and P contents of the macrophyte species to the comprehensive detritus decomposition. Data used for the initial C, N, and P contents were the PC_1 from the principal component analysis (PCA) on the nutrient contents of the three macrophytes and their mixtures, and data used for the comprehensive decomposition were the PC_1 from the PCA on accumulative dry mass losses and the amounts of C, N, and P released at 15 and 58 days. Arrows denote significantly positive relationships, with the width proportional to the strength of the relationship. The numbers adjacent to the arrows are standardized path coefficients. Goodness-of-fit statistics for the model are shown below. * $P < 0.05$, *** $P < 0.001$.

4. DISCUSSION

Global climate change scenarios for the coming 50−75 years predict that lake water temperatures will increase by up to 4 °C, together with an increase in extreme weather events.[4,43] In this study, we aimed to explore how a future climate scenario may affect the decomposition of macrophyte-derived detritus. Our experimental climate scenarios, including warming and temperature fluctuations, revealed the following two key findings. First, both a fixed increment warming and fluctuating warming significantly accelerated macrophyte detritus decomposition and C release. Second, there were species-specific asymmetric response patterns of N and P release dynamics to the different warming scenarios. These findings underscore the need to consider species-specific temperature characteristics in a future climate change scenario when assessing consequences of global warming on ecosystem processes.[14]

It is well established that temperature influences many biological processes including detritus decomposition.[15,17] Consistent with our predictions, future temperature scenarios, including a fixed increment warming and fluctuating warming treatments, accelerated macrophyte detritus dry mass loss and C release. Previous studies have demonstrated that moderate increases in temperature can significantly accelerate detritus decomposition in freshwater ecosystems.[14,15,24,44] Decomposition is a biological process controlled by the feeding and growth rates of microorganisms and macroinvertebrates although leaching is the key process in the decomposition of macrophytes during the initial exposure period.[45] Warming can stimulate microbial-mediated litter mineralization by affecting fungal and bacterial community structures,[14,24] respiration,[14,46] and enzyme activities.[25,26] In this study, we wanted to distinguish the effects of both a fixed increment warming and fluctuating warming, with a similar energy input, on macrophyte detritus decomposition. Although we hypothesized that fluctuating warming would have a greater impact on macrophyte dry mass loss and C release than a 4 °C rise in mean temperature, the lack of consistent differences in detritus remaining dry mass did not support this hypothesis. Instead, our results suggest that warming indirectly enhances macrophyte detritus dry mass loss and C release mainly by the amount of energy input rather than by the two modes by which warming was provided, i.e., through a mean increase and using a similar amount of energy but provided as fluctuating temperatures. One explanation might be that an increase in temperature, irrespective of the mode of delivery, enhances leaf litter leaching and reduces the negative effects of lignin in microbially driven decomposition.[47] Another nonexclusive explanation is that the effects of macrophyte species (i.e., detritus quality) on detritus decomposition are stronger than that of temperature treatments. In line with this, several studies have suggested that the initial litter characteristics are more important than environmental factors in decomposition processes,[17,20,31,45] and the litter decay rate of vascular plant may be highly dependent on litter C/N and C/P.[48] Albeit the temperature treatment significantly influenced detritus dry mass loss and C release, our results show that the initial litter characteristic of the macrophyte was more important than the temperature treatment in explaining macrophyte detritus decomposition. Thus, the differences in the effect of fixed

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increment warming and heat waves, with a similar energy input, on macrophyte detritus dry mass loss and C release may be masked by the effects of different macrophyte species.

In this study, our results showed that there were species-specific responses of N and P release dynamics to temperature treatments. The results further confirmed that the initial litter characteristics play an important role in the decomposition process.[49,50] Interestingly, we observed that there were noticeable differences between W and H treatments in the amounts of N and P released by the three macrophytes and the mixture, and there were asymmetric responses of the N and P release dynamics of *N. lutea*, *P. australis*, and the mixture to changes in the variability of warming conditions at different time points. It should be noted that the W and H treatments received approximately the same energy input during the entire study period so that any observed differences in the responses of N and P release to W and H treatments were due to fluctuations in temperature. The difference in the effects of W and H treatments on N and P release of macrophytes and species-specific asymmetric response patterns of N and P release dynamics to changes in the variability of warming conditions may be ascribed to the differences in bacteria and fungi species responses to temperature and litter quality.[14,18] Temperature and litter quality are known to be major drivers of microbial decomposer communities and thus of the dynamics of organic matter decomposition.[14,18,51] Previous studies have shown that an increase by 4 °C significantly reduced the diversity and density of the aquatic fungal community.[52] Moreover, a strong fungal species-specific response to temperature oscillations was observed in an 8 °C warming scenario[14] because different microorganism species have different temperature tolerance ranges.[53] A recent study also has demonstrated that the decomposition process can be greatly affected by bacteria−fungi interactions in response to litter quality and environmental factors, that bacteria involved in the decomposition of macrophyte litter are more sensitive to temperature variances, and that fungi have a higher specificity to the composition of plant materials.[18] The specific temperature sensitivity of dominant species of decomposers, and the communities they form, might therefore result in different responses of N and P release dynamics in different future climate scenarios.[14] Our findings therefore suggest that future climate scenarios may influence macrophyte detritus N and P release, which have the potential to inflict changes in C/N/P ratios in the water column.

In conclusion, different climate warming scenarios, including an increased frequency of heat waves, can significantly accelerate macrophyte detritus decomposition and C release. This release of C could boost and accelerate the browning of freshwaters and thereby affect productivity and biodiversity by drastically reducing the penetration of solar radiation into the water column.[54,55] More importantly, there are asymmetric responses of N and P release patterns to different future climate scenarios, and warming may lead to increases of N and P loads. There were significant differences in effects of fixed increment warming and heat waves on the amounts of N and P released from macrophyte-derived detritus. This may lead to alterations in N/P ratios in the water column, which may affect the structure and function of aquatic ecosystems, especially in the plankton community.[56,57] We acknowledge the limitations of experimental studies as true models of natural ecosystems and that experimental data should be interpreted with caution. However, such studies allow for replicated comparisons between control and treatment, thereby providing a complementary tool to modeling and monitoring of natural systems in understanding and predicting the direction and strength of the effects from future climate warming.[9,58] Many recent studies on heat waves have also shown that predicted alterations in future climate regimes may strongly influence both aquatic plant interactions and reproductive strategies,[7] predator−prey interactions in zooplankton,[59] dominance patterns among aquatic primary producers,[9] and benthic community.[60] Hence, our experimental scenario-approach provides a piece in the jigsaw puzzle of understanding and predicting macrophyte-derived detritus decomposition dynamics at different future climate change scenarios. Our results also highlight the importance of extreme climatic events when assessing the effect of global warming on ecosystem processes, such as decomposition and nutrient regeneration.

■ ASSOCIATED CONTENT

Supporting Information

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Original data of the manuscript in tabular form (XLSX)

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Notes

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