


Warming enhances sedimentation and decomposition of organic carbon in shallow macrophyte-dominated systems with zero net effect on carbon burial

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Abstract

Temperatures have been rising throughout recent decades and are predicted to rise further in the coming century. Global warming affects carbon cycling in freshwater ecosystems, which both emit and bury substantial amounts of carbon on a global scale. Currently, most studies focus on the effect of warming on overall carbon emissions from freshwater ecosystems, while net effects on carbon budgets may strongly depend on burial in sediments. Here, we tested whether year-round warming increases the production, sedimentation, or decomposition of particulate organic carbon and eventually alters the carbon burial in a typical shallow freshwater system. We performed an indoor experiment in eight mesocosms dominated by the common submerged aquatic plant *Myriophyllum spicatum* testing two temperature treatments: a temperate seasonal temperature control and a warmed (+4°C) treatment ($n = 4$). During a full experimental year, the carbon stock in plant biomass, dissolved organic carbon in the water column, sedimented organic matter, and decomposition of plant detritus were measured. Our results showed that year-round warming nearly doubled the final carbon stock in plant biomass from 6.9 ± 1.1 g C in the control treatment to 12.8 ± 0.6 g C (mean \pm SE), mainly due to a prolonged growing season in autumn. DOC concentrations did not differ between the treatments, but organic carbon sedimentation increased by 60% from 96 ± 9.6 to 152 ± 16 g C m^{-2} $year^{-1}$ (mean \pm SE) from control to warm treatments. Enhanced decomposition of plant detritus in the warm treatment, however, compensated for the increased sedimentation. As a result, net carbon burial was 40 ± 5.7 g C m^{-2} $year^{-1}$ in both temperature treatments when fluxes were combined into a carbon budget model. These results indicate that warming can increase the turnover of organic carbon in shallow macrophyte-dominated systems, while not necessarily affecting net carbon burial on a system scale.

KEYWORDS

carbon cycle, decomposition, global warming, mineralization, phenology, primary production, sedimentation, submerged aquatic plant

1 | INTRODUCTION

Inland waters are vital components of the global carbon cycle, by emitting carbon to the atmosphere, transporting it to the oceans and burying it in their sediments (Cole et al., 2007; Raymond et al., 2013). Globally, lakes are important carbon sinks, burying an estimated 0.03–0.25 Petagrams (10^{15} g) C each year (Cole et al., 2007; Mendonça et al., 2017). Small ponds also contribute substantially to the global carbon budget, despite their small size (Holgerson & Raymond, 2016). In small ponds, submerged macrophytes are an important structural component (Jeppesen, Sondergaard, Sondergaard, & Christofferson, 1998) and systems dominated by these aquatic plants have great potential for high carbon burial (Hilt, Brothers, Jeppesen, Veraart, & Kosten, 2017; Jeppesen et al., 2016). However, the efficiency of carbon burial can vary depending on environmental conditions such as oxygen availability (Sobek et al., 2009), latitude (Alin & Johnson, 2007), nutrient availability (Heathcote & Downing, 2012), and possibly temperature (e.g., Mendonça et al., 2016).

Temperature-dependency of carbon burial in macrophyte-dominated systems is of particular interest as global mean surface temperature is projected to increase over the coming century by 3–5°C (i.e., RCP 8.5 scenario in IPCC (2014)). Rapid warming of lakes has already been observed around the globe over the last decades (Adrian et al., 2009; Mooij, De Senerpont Domis, & Hülsmann, 2008; O'Reilly et al., 2015; Woolway et al., 2017). Temperature changes can modify the metabolic balance of freshwater lakes (Yvon-Durocher, Jones, Trimmer, Woodward, & Montoya, 2010), as aquatic respiration processes show a stronger response to warming than primary production (O'Connor, Piehler, Leech, Anton, & Bruno, 2009). Modifications to the metabolic balance in combination with increasing inorganic carbon loading from the catchment (Weyhenmeyer et al., 2015) can lead to enhanced dissolved carbon concentrations in already supersaturated lakes and ponds (Atwood et al., 2015; Flanagan & McCauley, 2010; Kosten et al., 2010) and decreased carbon burial efficiency (as suggested by Mendonça et al. (2016)) in warmer climates. Thus, a detailed understanding of how temperature affects carbon cycling on a system scale is important to predict how warming will influence the ratio between carbon emissions and burial in lakes (Mendonça et al., 2012). Currently, most studies focus on the effect of warming on overall carbon emissions from freshwater ecosystems, while net effects on carbon budgets may strongly depend on carbon burial in sediments.

Autochthonous carbon cycling can be divided into three main processes: the uptake of inorganic carbon by primary producers and its conversion into organic carbon bound in their biomass (net primary production), the subsequent sedimentation of senesced organic matter and the remineralization of organic carbon through decomposition (Yvon-Durocher, Allen, Montoya, Trimmer, & Woodward, 2010). Once arrived at the bottom of the lake, part of the sedimented organic material can be buried for a longer period of time in lake sediments. Each carbon-cycling process can depend on environmental conditions including lake temperature. Warming can enhance decomposition rates (Fernandes, Seena, Pascoal, & Cássio, 2014; Flanagan & McCauley, 2010; Gudas et al., 2010; Song, Yan, Cai, &

Jiang, 2013; Zhou, Chen, Yan, & Duan, 2016). Sedimentation of organic material can be positively (Kritzberg et al., 2014) or negatively (Flanagan & McCauley, 2008) affected by warming, most probably related to temperature-driven changes in primary production (Kritzberg et al., 2014). However, temperature-driven prolongation of growing seasons (Netten, Van Zuidam, Kosten, & Peeters, 2011) and changes in seasonal timing (Hansson et al., 2013; Velthuis, Domis et al., 2017; Zhang, Bakker, Zhang, & Xu, 2016), as well as shifts in vegetation type (Moss et al., 2011; Peeters et al., 2013) and plant carbon:nutrient stoichiometry (Velthuis, van Deelen, van Donk, Zhang, & Bakker, 2017), can also indirectly affect the impact of warming on aquatic carbon cycling. Understanding how temperature affects the intricate balance of primary production, sedimentation, and decomposition is essential for predicting carbon burial under global warming (Yvon-Durocher, Hulatt, Woodward, & Trimmer, 2017).

To our knowledge, no integrative studies on the effect of elevated temperature on submerged aquatic plant biomass and its fate via sedimentation and decomposition exist to date. Therefore, we tested the effect of warming on the carbon stocks in plant biomass and carbon fluxes in sedimentation and plant litter decomposition in a year-round ~1,000 L mesocosm experiment, stocked with Eurasian watermilfoil (*Myriophyllum spicatum* L.). *M. spicatum* is a submerged, rooted freshwater plant species native to Europe, Asia, and has spread to North America (Smith & Barko, 1990). The mesocosms were exposed to temperature scenarios representing temperate (Dutch) conditions and a +4°C scenario, representing the RCP 8.5 scenario (IPCC 2014). During the experiment, we measured plant abundance, as well as sedimentation and decomposition of particulate organic matter. We hypothesized that 4°C warming would prolong the growing season of *M. spicatum* by advancing its spring phenology and delaying its decline in autumn. We further hypothesized that the prolonged growing season would subsequently increase the production of particulate organic carbon and consequently enhance sedimentation. Similarly, temperature-driven increases in decomposition rates of plant litter were expected. To determine the net burial of autochthonously produced organic carbon over the course of the experiment, we integrated the sedimentation and decomposition fluxes into a carbon budget model.

2 | MATERIALS AND METHODS

2.1 | Experimental set-up

Eight 988 L indoor mesocosms referred to as limnotrons (1.35 m average depth, 0.97 m diameter, see also Verschoor, Takken, Mas-sieux, and Vijverberg (2003)) were filled on March 4, 2015 with 912 L of tap water (12.8 ± 7 and 0.85 ± 0.04 μ M DIN and DIP, respectively) and 75 L of pre-sieved sediment (5-mm mesh size) from the top layer (top 5 cm) of a mesotrophic shallow pond in Wageningen, The Netherlands (51°59'16.3"N 5°40'06.0"E). As this work was part of a 3-year mesocosm project, the sediment collected from the field was mixed with sediment from the experiment performed the year before (2–1 parts, v/v, for information on the previous experiment, see Frenken et al., 2016; Velthuis, Domis et al., 2017).

Prior to plant and nutrient additions, water was circulated between all mesocosms for 2 days to promote similar starting conditions. Five shoots of *Myriophyllum spicatum* (30 to 60-cm length, with attached roots), originating from the same mesotrophic pond as the sediment, were added on March 6, 2015 by attaching a small pebble to the stem and letting them sink to the bottom of the mesocosm. Due to initial limited growth of the plants, additional shoots were planted in the same manner on April 28 and June 30 (Supporting Information Table S1). Nutrients were added to the water column on March 9, 2015 to come to final concentrations of 52, 1.9 and 65 μM of NO_3^- , PO_4^{3-} and Si, respectively. The incident light at the water surface was kept constant throughout the experiment at 188 ± 5 (mean \pm SE) $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, provided by two HPS/MH lamps (CDM-TP Elite MW 315–400 W, AGRILIGHT B.V., Monster, The Netherlands). The light:dark cycle followed typical Dutch seasonality (Supporting Information Figure S1). Details on experimental conditions (TIC, pH, and nutrient availability) can be found in Supporting Information Table S2. Surface mixing during the experiment was achieved by an aquarium pump (EHEIM compact 300, EHEIM GmbH & Co. KG, Deizisau, Germany), positioned just below the water surface. Surface gas diffusion was promoted by two compact axial fans (AC axial compact fan 4850 Z, EBM-papst St. Georgen GmbH & Co. KG, Georgen, Germany) with an air flow of $100 \text{ m}^3 \text{ hr}^{-1}$.

Temperature treatments consisted of an average seasonal water temperature cycle (control) based on temperate climate conditions in the Netherlands (van Dam, 2009), and the same seasonal temperature cycle +4°C (warm), with $n = 4$ per treatment (Supporting Information Figure S1). Water temperatures were continuously monitored by PT100 temperature sensors at two depths and automatically adjusted by a computer-controlled custom-made climate control system (Specview 32/859; SpecView Ltd., Uckfield, UK). The experiment ran for a full year until March 14, 2016.

2.2 | Macrophyte PVI and biomass

Macrophyte abundance was recorded by weekly PVI (Percent Volume Infested, Canfield et al., 1984) estimates. Accordingly, plant height was measured with a ruler and cover (%) was estimated by eye in each mesocosm. From these measurements, the PVI of *M. spicatum* was calculated as:

$$\text{PVI} = \frac{\text{cover} * \text{height vegetation}}{\text{depth water column}}$$

After a full year, the experiment was terminated. Above- and belowground biomass was harvested and dried at 60°C until constant dry weight, weighed, and stored dry and dark until further analysis for elemental composition.

2.3 | Sedimentation

Sedimentation rates were determined each month by placing custom-made tube-shaped sedimentation traps (9-cm diameter, 18-cm

height, and 1.1-L volume) at one-meter depth (measured from the water surface) in the center of the mesocosm for a period of 3 days. The contents of the sediment trap (i.e., sedimented material and sestonic POC in the water inside the trap) were thereafter filtered over pre-washed GF/F filters (Whatman, Maidstone, UK), dried at 60°C overnight, and stored dry and dark for elemental analysis. To correct for sestonic POC (<220 μm), water samples were taken with a tube-sampler in the middle of the mesocosm on the same day as the sedimentation traps were taken out and handled in the same manner. Sedimentation rates (SRs) were calculated as the amount of sedimented POC (corrected for sestonic POC present inside the traps) divided over the time that the sedimentation traps hung in the mesocosms. The amount of sedimented organic carbon was then calculated as the area under the curve of these sedimentation rates.

2.4 | Decomposition

Microbial decomposition of sedimented macrophyte litter on the sediment surface was determined using a litterbag method (Benfield, 2006). A subset of *M. spicatum* plants was kept separately from the plants collected in the field for the inoculum of the experiment. Leaf and stem material from these plants were separated and dried at 60°C until constant dry weight. Polyester litter bags (10 \times 6 cm dimensions) with 515- μm mesh size (Top7even; Haarlem, the Netherlands) were filled with 0.5 g of dry stem or leaf material and hung in the mesocosms just above the sediment on May 7 (around the time when the plants started to grow). To correct for possible periphyton growth on the litterbags, empty bags were hung in the mesocosms as controls. After 15, 29, 68, 119, 182, and 249 days, one litterbag with leaf material, one with stem material, and two control litterbags were destructively sampled from each mesocosm. The bags were dried at 60°C until constant dry weight. The weight loss of the litterbags with plant material in them was corrected for the weight gain from the control litterbags. Plant material from the litterbags was stored dry and dark until elemental analysis. As we did not observe any sedimented stem material, we focus on the decomposition of leaf material. The results for the decomposition of stem material can be found in Supporting Information Figure S2.

To determine whether temperature affected dissolved oxygen concentrations near the sediment (and thereby oxygen availability for decomposition), oxygen was measured at the sediment interface (120-cm depth) every 2 weeks using a multi-parameter meter (HQ40d; Hach, Loveland, CO, USA) equipped with a luminescent dissolved oxygen (LDO) probe (IntelliCAL LDO101). Concentrations of dissolved organic carbon (DOC) were taken from filtered (0.15 μm) depth-integrated water samples on a monthly basis and analyzed on a TOC-L CPH/CPN analyzer (Shimadzu, Kyoto, Japan).

2.5 | Elemental analysis

The carbon (C) content was analyzed for the harvested plant biomass at the end of the experiment, as well as of sedimentation, sestonic, and decomposition samples throughout the experiment.

Furthermore, nitrogen (N) and phosphorus (P) content of the harvested macrophyte biomass and the sedimentation filters was analyzed. Dried above- and belowground macrophyte biomass was ground to a fine powder on a microfine grinder (MF 10 basic; IKA-werke, Staufen, Germany), while samples from the litterbags were ground in a test tube with a 1/8" ball bearing (Weldtite, Lincolnshire, UK) on a Tissuelyzer II (QIAGEN, Germantown, MD, USA). For the determination of C and N content from the seston and sedimentation samples, subsamples of approximately 13% were taken with a hole puncher from the respective GF/F filters and analyzed on a FLASH 2000 NC elemental analyzer (Brechtbuehler Incorporated, Interscience B.V., Breda, The Netherlands). Phosphorus content was determined according to Murphy and Riley (1962) by either combusting dry mass (macrophytes) or the remainder of the GF/F filters (sedimentation) in a Pyrex glass tube at 550°C for 30 min. Subsequently, 5 ml of persulfate (2.5%) was added and samples were autoclaved for 30 min at 121°C. Digested P (as orthophosphate) was measured colorimetrically on a QuAatro39 Auto-Analyzer (SEAL Analytical Ltd., Southampton, UK).

2.6 | Calculations and statistics

All calculations and statistics were carried out in R (R Core Team 2015), using the packages nlme, minpack.lm, stats, xlsx, and ggplot2 (Dragulescu, 2014; Elzhov et al., 2016; Pinheiro, Bates, DebRoy, & Sarkar, 2015; Wickham, 2010). All R-code is archived in the Dryad repository belonging to this paper. To determine whether warming advanced the spring phenology of *M. spicatum*, we determined the date at which half of the maximum PVI was recorded for each individual mesocosm (Rolinski, Horn, Petzoldt, & Paul, 2007; Zhang et al., 2016). When this cardinal date occurred between two sampling dates, we approximated it by linear extrapolation between these dates.

The carbon stock in the form of aboveground plant biomass at the end of the experiment was determined by multiplying dry weight with its carbon content for each individual mesocosm. To determine the decomposition rate and the fraction recalcitrant organic carbon (i.e., remaining carbon fraction) in the decomposition experiment, we used a two-phase decomposition model (as described by Harmon et al., 2009):

$$C_t = C_0 \times e^{-kt} + s$$

where C_0 is the initial fraction of organic carbon in the litter bags (= 1) and C_t the remaining fraction of organic carbon at time (t) since the start of the experiment (in days), k is the decomposition rate (in day^{-1}), and s is the fraction recalcitrant organic carbon. This decomposition model was fitted through the experimental data of leaf and stem litter for each individual mesocosm with the function *nlLM*, from which the parameters k and s were derived through nonlinear algorithms. The parameter decomposition rate (k) and recalcitrant fraction (s) were tested for differences between treatments using Student's t tests (function *t* test).

We used a carbon budget model to estimate the amount of autochthonously produced organic carbon during the experimental

year that was buried in the sediment of the mesocosm. In this model, we incorporated the dynamics of labile and buried particulate organic carbon throughout the season and assumed that the recalcitrant fraction s and the decomposition rate k determined from the decomposition dynamics are representative for the burial and decomposition rates of the sedimented carbon. With these parameters, we modeled the dynamics of labile organic carbon (LOC in g C/m^2) at the bottom of the system over the season for each individual mesocosm in the following manner:

$$\text{LOC}_t = \text{LOC}_{t-1} + (1 - s) \times \text{SR} \times \Delta t - \text{LOC}_{t-1} \times e^{-k\Delta t}$$

here, LOC is defined as the remainder of build-up of labile particulate organic carbon at the earlier time point, (LOC_{t-1}) plus the labile fraction ($1-s$) of the sedimented particulate organic carbon (at rate SR in day^{-1}) over the respective time interval (Δt in day^{-1}), minus the amount of organic carbon that was decomposed during that period (at rate k , in day^{-1}). For the dynamics in organic carbon burial (OCB in g C/m^2), the following equation was used for each individual mesocosm:

$$\text{OCB}_t = \text{OCB}_{t-1} + s \times \text{SR} \times \Delta t$$

here in, OCB is calculated as the recalcitrant fraction (s) of the sedimented organic carbon (at rate SR in day^{-1}) over the respective time interval (Δt in day^{-1}), plus the build-up of buried organic carbon at the earlier time point.

To test whether temperature treatment affected the dynamics over time of *M. spicatum* abundance (PVI), DOC concentrations, sedimentation of organic carbon, carbon:nutrient stoichiometry of the sedimented material, oxygen concentrations at the sediment and modeled LOC and OCB, linear mixed effect models were used (function *lme*). To account for multiple measurements in the same mesocosm over time (i.e., repeated measures), time nested within mesocosm identity was included as a random factor in the statistical model. Model residuals were checked for normality and homogeneity of variance and variables were transformed when necessary. p -values for treatment, time, treatment + time, and treatment \times time effects were obtained by pairwise comparison of the models that included those fixed effects (function ANOVA). To test whether warming affected the cardinal date of *M. spicatum* spring phenology, carbon pools and carbon:nutrient stoichiometry of macrophyte biomass, cumulative sedimented carbon at the end of the experiment, decomposition rates, and recalcitrant fractions of leaf and stem litter and the organic carbon burial (LOC+OCB) after a full experimental year, we used Student's t tests (function *t* test).

3 | RESULTS

3.1 | Macrophyte development, carbon stocks and carbon:nutrient stoichiometry

The abundance of *M. spicatum* gradually increased over the first 3 months of the experiment, until a maximum abundance of approximately 75% PVI was reached at the end of September in both

treatments. After this peak, abundance declined to 35% in the control treatment, while it remained around 65% PVI in the warm treatment. Over the entire experimental year, the abundance of *M. spicatum* was significantly higher in the warm treatment (Table 1). Furthermore, warming significantly affected spring phenology of plant growth as the date on which half of the maximum PVI was attained advanced by 10 days in the warm treatment (Student's *t* test; $t(3) = 3.9$, $p = 0.02$; Figure 1).

At the end of the experiment, the carbon stock in aboveground *M. spicatum* was 1.9-fold higher in the warm treatment compared to the control (Table 2). This carbon stock was significantly positively related to plant abundance (Linear regression, $R^2 = 0.88$, $p < 0.001$, $n = 8$, Supporting Information Figure S3). Warming did not affect macrophyte carbon content, aboveground C:P ratios, belowground carbon stocks, or belowground carbon:nutrient ratios. The aboveground C:N ratio of *M. spicatum* was 1.3 fold higher in the warm treatment compared to the control (Table 2). No effect of warming on dissolved organic carbon (DOC) concentrations could be detected (Supporting Information Figure S4, Table S3).

3.2 | Sedimentation

Sedimentation rates varied seasonally, with maximum rates at the end of August of 0.89 ± 0.20 and 1.70 ± 0.38 g C m⁻² day⁻¹ (mean \pm SE) in the control and warm treatment, respectively (Supporting Information Figure S5, Table S3). This sedimented material consisted mostly of detritus (unidentified particulate organic matter and senesced leaves of *M. spicatum*). The cumulative amount of sedimented organic carbon over the season was significantly higher in the warm treatment (Table 1; Figure 2). At the end of the experiment, 95.6 ± 9.5 and 152 ± 16 g C m⁻² had sedimented in the control and warm treatment, respectively (Table 2). Quality of the sedimented material was not significantly affected by warming, as carbon:nutrient ratios did not differ between treatments (Supporting Information Figure S6, Table 1). However, a gradual increase in these ratios was observed over the course of the experiment as indicated by a significant time effect. Oxygen concentrations at the sediment

TABLE 1 Summary of statistical analysis with linear mixed effect models, testing the effect of warming (treatment), time, and their interaction on *Myriophyllum spicatum* abundance, sedimentation, and the modeled carbon dynamics (LOC and OCB)

Variable	Unit	Log likelihood-ratio		
		Treatment	Time	Treatment \times time
Plant abundance				
<i>Myriophyllum</i> abundance	PVI	10.4**	148.4***	1.8
Sedimentation				
Cumulative sedimented organic carbon	g C m ⁻²	6.3*	225.1***	70.9***
C:P sedimented material	mol:mol	0.83	44.5***	9.1
C:N sedimented material	mol:mol	0.05	85.9***	13.9
Modeled carbon dynamics				
Labile organic carbon (LOC)	g C m ⁻²	5.2*	177.2***	20.2
Organic carbon burial (OCB)	g C m ⁻²	0.13	307.9***	0.63

Note. Significant outcomes are indicated in boldface, with * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

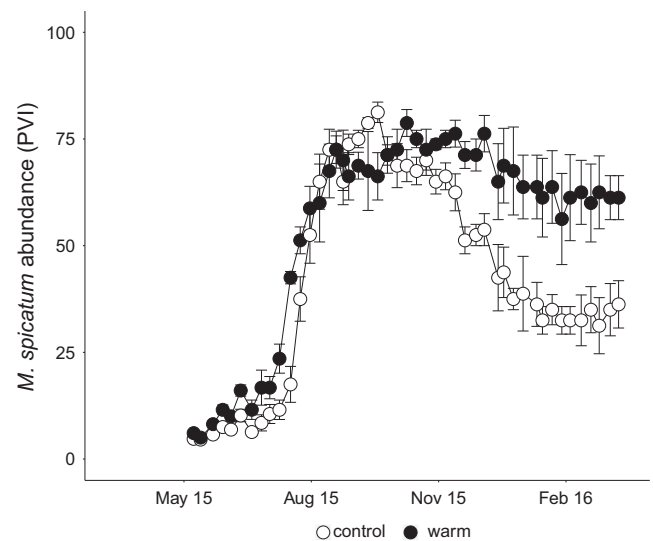


FIGURE 1 Development of *Myriophyllum spicatum* abundance over the experimental period in control (open circles) and warm (closed circles) treatments. Values represent mean \pm SE ($n = 4$)

did not differ between temperature treatments (Supporting Information Figure S7, Table S3).

3.3 | Decomposition

The fraction of carbon in plant leaf litter that was lost due to decomposition was significantly larger with warming, with the remaining fraction recalcitrant organic carbon (*s*) being 39% and 23% in the control and warm treatment (Figure 3, Table 2). No effect of warming could be detected on decomposition rates of leaf litter (*k*), which were 0.024 ± 0.0031 and 0.019 ± 0.0017 day⁻¹ in the control and warm treatment, respectively (Table 2).

3.4 | Modeled carbon burial dynamics

The carbon budget model showed that until September, labile organic carbon (LOC) accumulated on the sediment surface and

	Variable	Control	Warm	T-statistic (df)
Carbon pools	C stock in aboveground macrophyte biomass (g)	6.9 ± 1.1	12.8 ± 0.6	4.8 (4.6)**
	C stock in belowground macrophyte biomass (g)	0.4 ± 0.1	1.2 ± 0.5	1.6 (3.5)
Carbon:nutrient stoichiometry	Aboveground C content (% dryweight)	32.4 ± 1.0	31.6 ± 0.8	0.7 (5.7)
	Aboveground C:N (mol:mol)	19 ± 0.6	24 ± 0.9	4.5 (5.4)**
	Aboveground C:P (mol:mol)	337 ± 30.3	444 ± 40.3	2.1 (5.6)
	Belowground C content	37.9 ± 0.5	38.4 ± 0.3	1.1 (4.9)
	Belowground C:N (mol:mol)	27 ± 1.8	34 ± 2.6	2.1 (5.4)
	Belowground C:P (mol:mol)	424 ± 60	508 ± 51	1.0 (5.8)
Carbon fluxes	Cumulative sedimented organic carbon (g C m ⁻² year ⁻¹)	95.6 ± 9.6	152 ± 16	3.0 (4.9)*
	Fraction recalcitrant carbon leaf (s, unitless)	0.38 ± 0.023	0.24 ± 0.022	4.6 (6.0)**
	Decomposition rate leaf (k, day ⁻¹)	0.024 ± 0.0031	0.019 ± 0.0016	1.7 (4.4)
	Organic carbon burial (g C m ⁻² year ⁻¹)	41.2 ± 5.9	39.5 ± 6.4	0.2 (6.0)

TABLE 2 Summary of carbon pools, carbon:nutrient stoichiometry, and carbon fluxes in the control and warm treatment (mean ± SE, $n = 4$) at the end of the experiment and the output of Student's t tests (T -statistics and degrees of freedom [df]), determining differences between treatments

Note. Significant differences between treatments are indicated in boldface, with ** $p < 0.01$ and * $p < 0.05$.

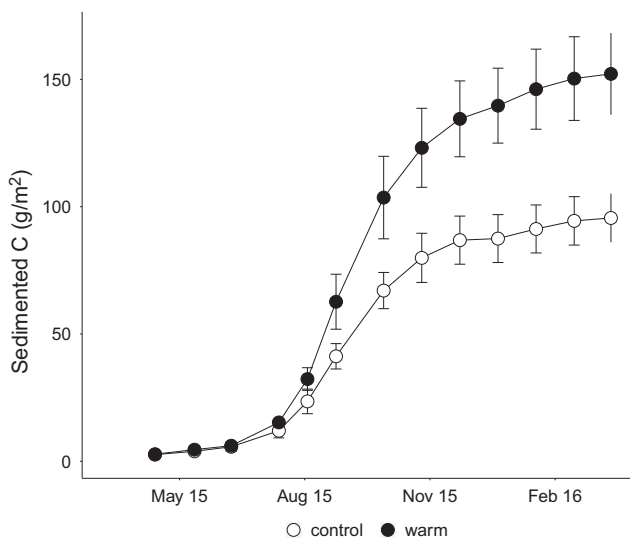


FIGURE 2 Cumulative amount of sedimented organic carbon in the control (open circles) and warm (closed circles) treatments. Values represent mean ± SE ($n = 4$)

thereafter decreased in both treatments (Figure 4a). The amount of LOC throughout the experiment was higher in the warm treatment than in the control, while organic carbon burial (OCB) did not differ between treatments (Table 1). However, there was a significant time effect on organic carbon burial, indicating its accumulation over the experiment (Figure 4b). The amount of remaining organic carbon in the sediment (LOC + OCB) after a full experimental year was 41.2 ± 5.9 and 39.5 ± 6.4 g C m⁻² in the control and warm

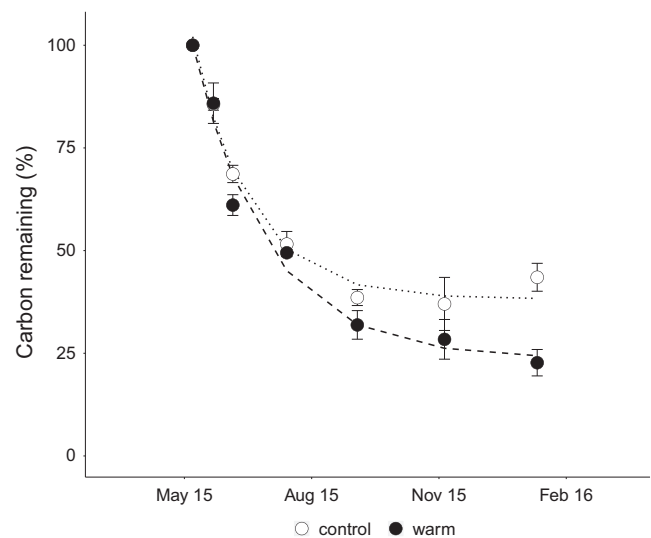


FIGURE 3 Percentage of remaining carbon in decomposing leaf litter of *M. spicatum* during the experiment, in control (open circles) and warm (closed circles) treatments. Values represent mean ± SE ($n = 4$). Treatment specific fits of the two-phased decomposition model are indicated by the dotted (control) and dashed (warm) line treatment, respectively. No effect of warming on this organic carbon burial was found (Table 2).

4 | DISCUSSION

Global warming is predicted to have strong impacts on the carbon balance in aquatic ecosystems (Yvon-Durocher, Allen et al., 2010).

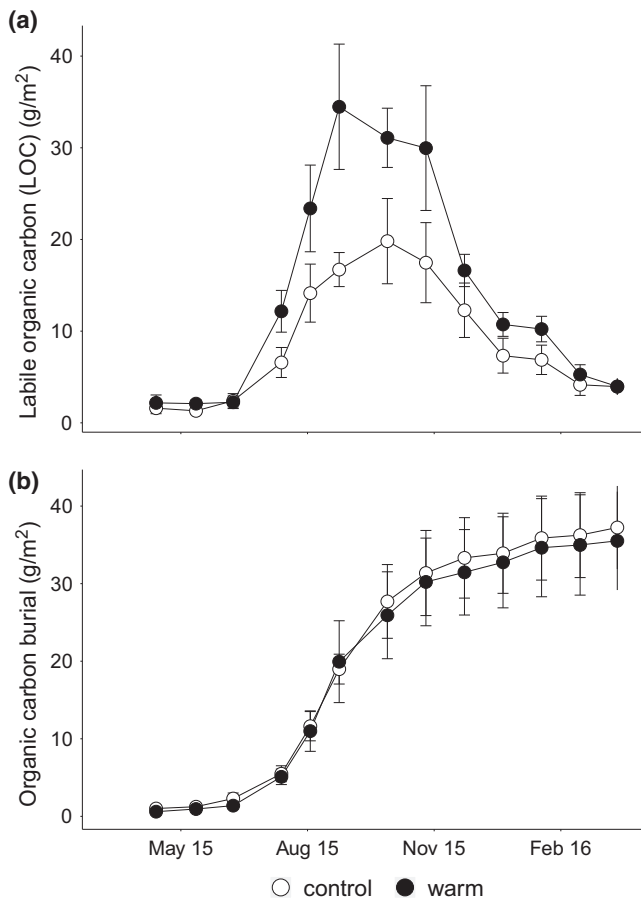


FIGURE 4 Modeled dynamics of labile organic carbon (a) and organic carbon burial (b) in the sediment over time, with control (open circles) and warm (closed circles) treatments. Values represent mean \pm SE ($n = 4$)

Our findings demonstrate that 4°C year-round warming leads to a prolonged submerged macrophyte growing season, and an elevated organic carbon stock in aboveground plant biomass, but not an enhanced DOC concentration. In accordance with the increased plant biomass, we observed that the sedimentation of particulate organic matter also increased. Decomposition of leaf litter was more complete in the warm treatment. The decomposition and sedimentation processes, however, counterbalanced each other in such a way that organic carbon burial was similar in both temperature treatments (Figure 5). Warming can thus significantly enhance the turnover of particulate organic carbon in temperate, plant-dominated freshwater systems, while organic carbon burial and thereby longer-term storage in sediments can remain unaffected.

4.1 | Warming effects on submerged plant abundance and DOC concentrations

As warming can accelerate growth rates of organisms and prolong their growing seasons (Brown, Gillooly, Allen, Savage, & West, 2004; Netten et al., 2011; Peeters et al., 2013), a positive response of warming on standing stock biomass of *Myriophyllum spicatum* was

anticipated in our experiment. Indeed, the abundance of *M. spicatum* was significantly higher in the warm treatment throughout the experiment even though more initial biomass was added to the control treatment (Supporting Information Table S1). Higher *M. spicatum* abundance in the warm treatment is most probably attributed to higher production rates, as indicated by enhanced sedimentation rates in the warm treatment. Warming has been shown to enhance the growth of *M. spicatum* (Li et al., 2017), as well as of other aquatic (Barko & Smart, 1981; Kaldy, 2014; Peeters et al., 2013; Velthuis, van Deelen et al., 2017) and terrestrial plants (Rustad et al., 2001), indicating that this is a common response across ecosystems.

Additionally, warming can advance the spring phenology of aquatic (Hansson et al., 2013; Velthuis, Domis et al., 2017; Winder & Schindler, 2004; Zhang et al., 2016) and terrestrial organisms (Parmesan, 2007). Indeed, we detected an advanced spring phenology and an additional delayed decrease of *M. spicatum* abundance under warmed conditions underlying the observed differences in *M. spicatum* abundance between our treatments. Our findings support a prolonged growing season under climatic warming, which can be observed in a multitude of natural systems (Walther et al., 2002). Such temperature-induced changes in the length of growing seasons may in turn have consequences for aquatic carbon cycling, as prolonged presence of macrophytes indicates an extended manifestation of that respective carbon stock. The carbon stock in *M. spicatum* aboveground biomass at the end of the experiment was indeed higher in the warm treatment. As no differences in carbon content were observed between temperature treatments, this enhanced carbon stock with warming is attributed to higher macrophyte biomass. Thus, through increased growth and a longer growing season of submerged plants, warming can lead to a higher carbon stock in the form of plant biomass.

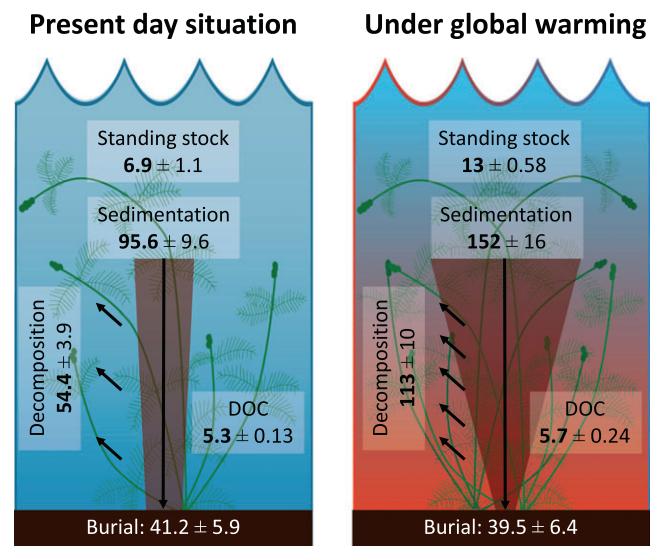


FIGURE 5 Summary of autochthonously produced organic carbon pools and fluxes (mean \pm SE) in macrophyte-dominated systems in the present-day situation (control) and under global warming (warm), with standing stock (macrophyte biomass) at the end of the experiment in g C, DOC in g C and sedimentation, decomposition, and burial in g C/m²/y

Although not the main focus of this study, dissolved organic carbon (DOC) concentrations can be an outcome of leaching from aquatic primary production (Barrón, Apostolaki, & Duarte, 2012) and consequently a temperature-induced increase related to enhanced macrophyte biomass was anticipated. However, no effect of warming on DOC concentrations was observed (Figure 5), which may be due to simultaneous temperature-driven increases in DOC mineralization rates (Gudasz et al., 2010). Nonetheless, a climate change-related increase in DOC concentrations is to be expected in lakes, often linked to enhanced DOC inflow from the catchment area (Larsen, Andersen, & Hessen, 2011).

4.2 | Warming effects on sedimentation

Warming-induced increases in primary production can promote the sedimentation of organic carbon (Kritzberg et al., 2014). Indeed, the amount of sedimented organic carbon was higher in the warm treatment, indicating enhanced production of particulate organic carbon with warming. The annual sedimentation rate in our mesocosms ($96\text{--}152\text{ g C m}^{-2}\text{ year}^{-1}$; Figure 5) falls within the range of sedimentation rates measured in lakes worldwide ($4\text{--}400\text{ g C m}^{-2}\text{ year}^{-1}$; Tartari and Biasci, 1997). To our knowledge, these are the first empirical results to address the effects of warming on sedimentation rates in a macrophyte-dominated freshwater system and our findings demonstrate a way in which warming may increase the carbon flux to lake sediments. Conflicting findings are reported for plankton dominated systems, where 3–4 degrees of warming can lead to an increase (Kritzberg et al., 2014) or decrease (Flanagan & McCauley, 2008) in sedimentation of organic carbon. This discrepancy in warming effects on sedimentation rates may be attributed to the presence of grazers and the top-down control they impose on the carbon stocks in primary producers (Flanagan & McCauley, 2008). As roughly 90% of the consumed organic material by grazers can be respired as CO_2 , their presence introduces a loss of organic carbon from the system (Yvon-Durocher, Allen et al., 2010). In our experiment, no grazing on *M. spicatum* was observed. On the contrary, warming positively affected macrophyte biomass. As dense macrophyte stands can reduce flow velocity (Madsen, Chambers, James, Koch, & Westlake, 2001), this temperature-driven increase in macrophyte biomass could in theory indirectly enhance sedimentation rates by reducing resuspension of the sediment (Jeppesen et al., 1998). However, as flow velocity did not play a strong role in our mesocosm experiment, we prefer to attribute the positive effect of warming on carbon sedimentation to enhanced production of organic material (Kritzberg et al., 2014).

4.3 | Warming effects on decomposition

Decomposition rates of leaf litter in our experiment were around 0.02 day^{-1} , which is in the same range as field surveys with *M. spicatum* ($0.01\text{--}0.06\text{ day}^{-1}$; Carpenter and Adams, 1979) and other aquatic macrophytes ($0.0008\text{--}0.06\text{ day}^{-1}$; Chimney and Pietro, 2006). In our experiment, the water at the sediment surface where

litterbags were exposed remained oxic in both treatments (Supporting Information Figure S7). Anaerobic conditions as often observed below dense macrophyte stands and in the sediment (Frodge, Thomas, & Pauley, 1990; Sukhodolova, Weber, Zhang, & Wolter, 2017) would likely have led to lower decomposition rates than we observed. This could in turn also have altered the balance between sedimentation and decomposition found in our study, resulting in a possible overestimation of decomposition rates under varying oxygen conditions.

Warming significantly reduced the remaining carbon in leaf litter decomposition. This enhanced decomposition is in line with temperature-induced increases in the degree of decomposition of other aquatic plants (Carvalho, Hepp, Palma-Silva, & Albertoni, 2015; Passerini, Cunha-Santino, & Bianchini, 2016; Song et al., 2013), as well as allochthonous leaf litter in aquatic systems (Fernandes et al., 2014) and soil respiration in terrestrial ecosystems (Rustad et al., 2001). Surprisingly, no effect of warming on the decomposition rate k could be detected in our experiment, as the observed results were driven by a lower remaining fraction recalcitrant carbon (s), which was 14% lower in the warm treatment. The unaffected decomposition rates are possibly a result of the relative short time span of the decomposition experiment, leading to overestimations of the recalcitrant fraction (Koehler, Wachenfeldt, Kothawala, & Tranvik, 2012). Alternatively, our findings could stem from a higher temperature sensitivity of this recalcitrant material to decomposition (Davidson & Janssens, 2006), which in turn can be caused by temperature-driven community shifts toward decomposers that can degrade more recalcitrant organic matter (Dang, Schindler, Chauvet, & Gessner, 2009) and a higher activity of enzymes needed for this recalcitrant matter degradation (Ylla, Romani, & Sabater, 2012).

As the experiment presented here was conducted over a 1-year period, possible long-term effects of warming on litter decomposition were not taken into account. For instance, sedimentation of the enhanced macrophyte biomass in the warm treatment may lead to rapid changes in sediment redox conditions and related oxygen concentrations, thereby potentially reducing decomposition rates (Passerini et al., 2016). Furthermore, recalcitrant carbon is not necessarily static and can decompose further over a timespan of years, although at a much slower rate than its labile counterparts (Koehler et al., 2012). Relatedly, we may have overestimated the fraction of recalcitrant organic material in the warm treatment as at the end of the experiment the fraction still seemed to decrease, while the decomposition seems to have stabilized in the control treatment (see Figure 3). This would imply an underestimation of the effect of warming on decomposition.

4.4 | Warming effects on organic carbon burial

Net organic carbon burial was determined by combining particulate organic carbon fluxes by sedimentation and decomposition into a carbon budget model. This model showed that the individual carbon fluxes counteracted each other in such a way that organic carbon burial was unaffected by 4°C warming. In other words, warming

stimulated the carbon turnover rate by enhancing both sedimentation and litter decomposition fluxes. Temperature-driven increases in carbon turnover can also be observed in terrestrial ecosystems (Knorr, Prentice, House, & Holland, 2005) and thus seem to be a common response to warming across ecosystems. We calculated an average organic carbon burial rate of $40 \text{ g C m}^{-2} \text{ year}^{-1}$ which falls within the spectrum of burial rates determined for European lakes ($0.1\text{--}58 \text{ g C m}^{-2} \text{ year}^{-1}$; Kastowski, Hinderer, and Vecsei, 2011). Furthermore, our model indicates clear seasonal dynamics in the balance between sedimentation and litter decomposition. Until September, labile organic carbon (LOC) accumulated in the sediment in both treatments, as sedimentation rates were larger than decomposition rates (see Figure 2 and Table 2). Simultaneously, the pool of labile organic carbon was enhanced by warming, because of the prolonged growing season and related higher abundance of *M. spicatum* in the warm treatment, leading to enhanced sedimentation rates. However, the calculated amount of organic carbon in the sediment decreased from September onwards, as the decomposition rate was higher than the sedimentation rate in this period. Finally, the organic carbon burial at the end of the year did not differ between treatments. Thus, even though more carbon sedimented in the warm treatment, a greater proportion of this sedimented carbon was subsequently respired through decomposition.

Our carbon budget model does not take changes in litter quality in response to warming into account. Litter quality (expressed as for instance carbon:nutrient ratios) can be an important determinant for decomposition, where decomposition rates increase with increasing quality (Cebrian & Lartigue, 2004; Handa et al., 2014; Zhang, Hui, Luo, & Zhou, 2008). Warming can lead to shifts in carbon:nutrient ratios of aquatic plants (Ventura et al., 2008; Zhang et al., 2016), but the direction of change is not uniform across studies (Velthuis, van Deelen et al., 2017). In our experiment, aboveground plant C:N ratios were higher in the warm treatment compared to the control (Table 2), indicating a decreased quality of these plants. As our carbon budget model assumes a fixed litter quality, we may in theory overestimate the effect of warming on litter decomposition. Nonetheless, decomposition rates of leaf and stem litter of *M. spicatum* were similar, even though those litter types differed in carbon:nutrient ratios (Supporting Information Figure S2). Furthermore, the quality of the sedimented material did not differ between temperature treatments (Supporting Information Figure S6). Thus, even though litter quality is an important factor to consider in decomposition dynamics, it seems not to be a major driver of temperature effects on decomposition in this particular experimental set-up.

The fate of organic carbon in the sediment is determined by the carbon burial efficiency, which is the balance between buried and sedimented carbon. Fast accumulation of sedimented carbon can lead to higher carbon burial efficiency, as this can reduce oxygen exposure time at the sediment surface (Mendonça et al., 2016; Sobek et al., 2009). Overall, the carbon burial efficiency was 43% in our control treatment and—corresponding with the high turnover—only 26% in the warm treatment. These percentages are lower than for lakes that receive important allochthonous carbon inputs, but

they fall within the range found for lake sediments that receive mainly autochthonous produced carbon (Sobek et al., 2009).

4.5 | Upscaling from mesocosms to more complex systems

Even though mesocosm systems are a valuable experimental approach to climate change research, it is by definition limited in complexity and our future ecosystems will inevitably have to deal with a complex array of environmental pressures not present in our mesocosm system. Therefore, future research should build upon our current experimental approach by increasing this complexity. Possible next steps would be to expand to aquatic systems of differing morphology and add a terrestrial subsidy of organic carbon to test the relationship between warming and carbon burial in more multifaceted systems. Such systems could include various macrophyte species, herbivores, and other higher trophic levels and ultimately upscale to the landscape level.

4.6 | Conclusions and implications

With the predicted climatic warming over the coming century and its potential feedbacks on the global carbon cycle, temperature-driven changes in freshwater carbon cycling are an important component of climate change research (Yvon-Durocher, Allen et al., 2010). Highly productive macrophyte-dominated freshwater systems (Kazanjian et al., 2018) play an important role in long-term carbon storage at the landscape (Premke et al., 2016) and even at the global scale (Mulholland & Elwood, 1982). Our experimental results suggest that 1 year of 4°C warming will increase production and sedimentation of organic carbon in these systems. Assuming that autochthonous carbon production is the main form of carbon influx, enhanced decomposition with warming can compensate for the increased sedimentation of this organic carbon. Climatic warming may thus increase the turnover rate of aquatic carbon cycling, while not necessarily affecting net carbon burial on a system scale.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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