Global-change effects on early-stage decomposition processes in tidal wetlands – Implications from a global survey using standardized litter

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Abstract

Tidal wetlands, such as tidal marshes and mangroves, are hotspots for carbon sequestration. The preservation of organic matter (OM) is a critical process by which tidal wetlands exert influence over the global carbon cycle and at the same time gain elevation to keep pace with sea-level rise (SLR). The present study assessed the effects of temperature and relative sea level on the decomposition rate and stabilization of OM in tidal wetlands worldwide, utilizing commercially available standardized litter. While effects on decomposition rate per se were minor, we show strong negative effects of temperature and relative sea level on stabilization, as based on the fraction of labile, rapidly hydrolyzable OM that becomes stabilized during deployment. Across study sites, OM stabilization was 29% lower in low, more frequently flooded vs. high, less frequently flooded zones. Stabilization declined by ~75% over the studied temperature gradient from 10.9 to 28.5°C. Additionally, data from the Plum Island long-term ecological research site in Massachusetts, US show a pronounced reduction in OM stabilization by >70% in response to simulated coastal eutrophication, confirming the potentially high sensitivity of OM stabilization to global change. We therefore provide evidence that rising temperature, accelerated SLR, and coastal eutrophication may decrease the future capacity of tidal wetlands to sequester carbon by affecting the initial transformations of recent OM inputs to soil OM.

1   Introduction

Tidal wetlands, such as marshes and mangroves, provide a wide array of ecosystem services that have been valued at approximately US\$ 10,000 per hectare and year, making them some of the most economically valuable ecosystems on earth (Barbier et al., 2011; Kirwan and Megonigal, 2013). Yet, tidal wetlands are threatened and vulnerable ecosystems, experiencing pronounced loss though global-change impacts, such as land use (Pendleton et al., 2012) and accelerated sea-level rise (SLR) (Craft et al., 2009; Crosby et al., 2016). In recent years, carbon sequestration has increasingly been recognized as an ecosystem service of tidal wetlands (Chmura et al., 2003; Mcleod et al., 2011). Here, high rates of organic matter (OM) input (from both autochthonous and allochthonous production) co-occur with reducing soil conditions and thus slow rates of decomposition, leading to long-term carbon-sequestration rates that exceed those of most other ecosystem types by an order of magnitude (Mcleod et al., 2011). At the same time, suppressed decomposition and the preservation of OM is a primary process by which many tidal wetlands gain elevation and keep pace with rising sea level (Kirwan and Megonigal, 2013). Consequently, global changes that decrease OM preservation in tidal-wetland soils not only affect carbon sequestration, but also decrease ecosystem stability against SLR. It is therefore critical to identify global-change factors that affect the transformation of organic inputs to stable soil OM (SOM) in tidal wetlands and to assess the magnitude of their effects.

There are multiple methods for assessing factors that influence carbon sequestration, including direct measurements of plant production, carbon stocks, accretion, and decomposition rates. Litter-bag techniques assessing the weight loss of plant material over time are probably the easiest way to measure decomposition rates in situ and have been widely used since the 1960s (Prescott, 2010). Global-scale assessments of litter decomposition have been conducted as both meta-analyses (e.g. Zhang et al., 2008) and as inter-site studies along latitudinal gradients (Berg et al., 1993; Cornelissen et al., 2007; McTiernan et al., 2003; Powers et al., 2009; Trofymow et al.,

2002) in order to assess effects of climate parameters on decomposition rate. Besides abiotic or climate effects, these studies could also identify litter quality itself as an important predictor for decomposition rate (Zhang et al., 2008).

Relationships between single climate or litter-quality parameters and decomposition rate

100   often are not linear. Instead, complex interactions between litter-quality and climate parameters seem to control litter decomposition (Zhang et al., 2008), creating challenges in separating climate from litter-quality effects and predicting the relevance of potential global-change drivers for decomposition rate. In order to separately assess environmental or climate effects on litter decomposition at a global scale, it is therefore necessary to standardize litter quality in inter-site

105   studies. However, implications of litter-decay data for carbon sequestration need to be considered cautiously, as the link among litter-decomposition rate, SOM formation, and ultimately carbon sequestration is not straightforward (Cotrufo et al., 2013; Prescott, 2010): Because plant tissues are not resistant to decay per se, it is critical to understand their biogeochemical transformation into stable compounds that leads to the formation of SOM (i.e. stabilization) rather than understanding

110   the pace at which early-stage decomposition proceeds (Castellano et al., 2015; Haddix et al., 2016; Prescott, 2010).

Keuskamp and others (2013) developed an efficient approach for studying litter decomposition and OM transformation at a global scale, using commercially available tea as standardized material. Their Tea Bag Index (TBI) approach is based on the deployment of two types

115   of tea that considerably differ in their OM quality. The method allows for the determination of the decomposition rate constant (in the following referred to as *decomposition rate* or k) and a stabilization factor (in the following referred to as *stabilization* or S), which describes the fraction of labile and rapidly decomposable OM that becomes stabilized during deployment.

In the present study, we assessed effects of the global-change factors global warming,

120   accelerated SLR, and coastal eutrophication on both OM decomposition rate and stabilization in

tidal-wetland soils by conducting a worldwide survey using standardized litter. First, by covering a

large temperature gradient of $\Delta T > 15$ °C across sites, we aimed to capture temperature effects on

OM decomposition rate and stabilization, thereby improving our understanding on how global

warming affects carbon turnover and ultimately sequestration in tidal wetlands. Second, by

125   conducting paired measurements in both high- and low-elevated zones of tidal wetlands worldwide,

we were aiming to gain insight into potential effects of accelerated SLR on carbon turnover. Despite

the dominant paradigm that decomposition is inversely related to flooding, the existing literature on

hydrology and SLR effects on OM decomposition in tidal wetlands yields equivocal results, which

is often due to the overriding effect of OM quality on decomposition rate (Hemminga and Buth,

130   1991; Kirwan et al., 2013; Mueller et al., 2016). Lastly, we used the TIDE project plots of the Plum

Island long-term ecological research site in Massachusetts, US (Deegan et al., 2012) to

experimentally assess both the effects of coastal eutrophication and – with respect to SLR-driven

increases in flooding frequency – the relevance of nutrient delivery through floodwater for the early

stages of OM decomposition in tidal wetlands.

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 2 **Methods**

2.1 Study sites and experimental design

The worldwide survey was conducted during the 2015 growing season and included a total of 30

tidal-wetland sites. Sites were partly co-located within larger coastal and estuarine regions (Fig. 1,

Table 1). Eleven sites were situated along the European coasts of the North Sea, Mediterranean, and

150 Baltic, Thirteen sites were located along the East and West coasts of North America including the

St. Lawrence Estuary, Bay of Fundy, Chesapeake Bay, and San Francisco Bay, and four mangrove

sites were situated along the Caribbean coast of Central America in Belize and Panama.

Additionally, one Chinese site (Yangtze Estuary) and one Argentinian site were included in our

study. Sixteen of the sites were salt marshes, ten were tidal freshwater and brackish sites, and four

155 sites were mangroves. In 21 sites, we compared high and low elevated zones, which were

characterized by distinct plant species compositions (i.e. different communities in high vs. mid vs.

low marshes) or by different stature of mangroves (i.e. dwarf vs. fringe phenotypes). We used

relative elevation (i.e. high vs. low elevated zone) as a site-specific proxy for relative sea level. By

doing so, we did not capture the actual variability in the tidal inundation regime across our study

160 sites as these vary in absolute elevation and in elevation relative to mean high water. Finally, we

included the long-term experimental site of the TIDE project in Massachusetts, US to assess effects

of nutrient enrichment on litter-decomposition rate and stabilization. Through nitrate additions to

the incoming tides on at least 120 days per year, nutrient enriched areas at the TIDE project site

receive floodwater with 10-15 fold increased nitrogen (N) concentrations compared to reference

165 areas since 2004. From 2004-2010 also phosphate was added to the floodwater; however, this has

been discontinued because creek water P concentrations are high enough to prevent secondary P

limitation through N enrichment (details in Deegan et al., 2012; Johnson et al., 2016).

Decomposition rate and stabilization were measured by deploying tea bags in ten points per

zone (or treatment) within a site (n = 10). Spacing between replicates within a zone (or treatment)

170   was ≥2 m. However, as sites differed considerably in their areal extent, the distribution and thus

spacing between points had to be adjusted to be representative for the given system. Air temperature

for the period of deployment was measured at site, or temperature data was obtained from the online

service of *AccuWeather* (accuweather.com; accessed 12/25/2016) for locations within a distance of

15 km to the site for most sites, but not further than 60 km for some remote sites. It needs to be

175   noted here, that top-soil temperature would differ from air temperature depending on factors such as

canopy shading or tidal regime and water temperature. As a consequence, air temperature can only

approximate the temperature conditions of the actual decomposition environment (Fig. S2).

2.2   Decomposition-rate and stabilization measurements

180   Decomposition rate (k) and stabilization (S) were assessed following the TBI protocol (Keuskamp et

al., 2013). The TBI approach can be considered as a simplified litter-bag approach, allowing a time-

and cost-efficient characterization of the decomposition environment, because k and S can be

estimated without repeated sampling of the decomposing material as in conventional approaches.

This implies the assumptions that (1) S is equal for the two types of material used in the approach

185   and (2) that decomposition of non-hydrolyzable materials during the 3 months of deployment is

negligible. We refer the reader to Keuskamp et al. (2013) for further detail and validity assessments

of assumptions.

      At each measuring point, two nylon tea bags (200 µm mesh size), one containing green tea

(EAN: 8 722700 055525; Lipton, Unilever, UK) and one containing rooibos (8 722700 188438,

190   Lipton, Unilever, UK), were deployed as pairs in ~8 cm soil depth, separated by ~5 cm. The initial

weight of the contents was determined by subtracting the mean weight of ten empty bags (bag +

string + label) from the weight of the intact tea bag prior to deployment (content + bag + string +

label). The tea bags were retrieved after an incubation time of 92 ± 6 (SD) days, with three sites

having an incubation period >100 days and one site <80 days. Upon retrieval, tea bags were opened,

195   and tea materials were carefully separated from fine roots and soil, dried for 48 h at 70°C, and

weighed.

Calculations for *k* and *S* followed Keuskamp et al. (2013):

Eq 1) $W_r(t) = a_r\, e^{-kt} + (1-a_r)$

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Eq 2) $S = 1 - a_g / H_g$

Eq 3) $a_r = H_r\, (1-S)$

205    $W_r(t)$ describes the substrate weight of rooibos after incubation time (*t* in days), a_r the labile and $1-a_r$

the recalcitrant fraction of the substrate, and *k* is the decomposition rate constant. *S* describes the

stabilization factor, a_g the decomposable fraction of green tea (based on the mass loss during

incubation) and H_g the hydrolyzable fraction of green tea. The decomposable fraction of rooibos tea

is calculated in Eq 3 based on its hydrolyzable fraction (H_r) and the stabilization factor *S*. With

210    $W_r(t)$ and a_r known, *k* is calculated using Eq 1.

In accordance with Keuskamp et al. (2013), extractions for determination of the

hydrolyzable fractions of green and rooibos tea followed Ryan et al. (1990). However, instead of

using Ryan's *forest products protocol* we conducted the alternative *forage fiber protocol* for the

determination of the hydrolyzable fraction. Briefly, 1 g of dried tea material (70°C for 24 h) was

215   boiled in cetyltrimethyl ammonium bromide (CTAB) solution (1 g CTAB in 100 ml 0.5 M H_2SO_4)

for 1 h (Brinkmann et al., 2002; Ryan et al., 1990). The extract was filtered through a 16-40-µm

sinter filter crucible (Duran, Wertheim, Germany) using a water-jet vacuum pump and washed with

150 ml of hot water followed by addition of acetone until no further de-coloration occurred

(Brinkmann et al., 2002). The remaining material was left in the sinter, dried for 12 h at 70°C,

220 cooled in a desiccator and weighed. 20 mL of 72% H_2SO_4 was added to the sinter and filtered off

after an incubation of 3 h, followed by washing with hot water to remove remaining acid. The sinter

was dried at 70°C for 12 h, cooled in a desiccator, and weighed to determine the non-hydrolyzable

fraction. Finally, the sinter containing the remaining sample was ignited at 450°C for 3 h in order to

determine the ash content of the material.

225   In addition to the determination of the hydrolyzable fraction, we measured total C and N

contents of the tea material using an elemental analyzer (HEKAtech, Wegberg, Germany). The

hydrolyzable fraction of both green and rooibos tea was higher than reported in Keuskamp et al.

(2013) (Table S1). However, the determined C and N contents of the tea materials are in agreement

with those reported in Keuskamp et al. (2013) (Table S1). Therefore, deviations from the

230 hydrolyzable fraction as reported previously are likely due to the less conservative extraction

assessment in the present study and not due to actual changes in the quality of the materials.

2.3   Data mining

Relationships between single parameters and litter decomposition are often not linear. Instead,

235 critical thresholds seem to exist at which a certain predictor (e.g. mean annual temperature)

becomes influential (Prescott, 2010; Rothwell et al., 2008). In the first step of data mining, we

therefore used classification and regression tree analysis (CART) to identify potential thresholds

and important predictors for *k* and *S* (Fig. S1). Data mining was conducted using STATISTICA 10

(StatSoft Inc., Tulsa, OK, USA).

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2.4   Statistical analyses

To test for effects of temperature on *k* and *S*, Spearman rank correlations were conducted using site

means (n = 30). As we did not expect temperature to be independent of other parameters in this

observational study, we constructed a Spearman correlation matrix including the parameters

245   temperature, latitude, tidal amplitude, salinity class, k, and S. Additionally, we tested for differences

in these parameters between marshes and mangroves and sites with mineral and organic soils, using

Mann-Whitney U tests (Table 2). Curve fitting was used to further explore relationships between

temperature, k, and S, and regression models with lowest standard error of estimate and highest R^2

are displayed in Figure 2 and 3.

250   To test for effects of relative elevation (as proxy for relative sea level) on k and S, two-tailed

paired t-tests were conducted. Mean values of high and low elevated zones of the 21 sites where tea

bags were deployed in both high and low elevation zones were used (n = 21). The absence of

outliers and normal distribution of the difference in the independent variable (as assessed visually)

assured robustness of paired t-tests. To assess the consistency of potential effects of relative

255   elevation on k and S, one-way ANOVAs were used in each site separately (replication was

sufficient in 20 sites). Normal distribution of residuals was assessed visually, Levene's test was

used to test for homogeneity of variance, and data were log-transformed if assumptions were not

met. Mann-Whitney U tests were conducted as a non-parametric alternative when log-transformed

data did not meet ANOVA assumptions (Table S2).

260   We tested for effects of nutrient enrichment on k and S in the data from the TIDE project site

(Massachusetts, US) using two-way ANOVA with enrichment treatment and marsh zone as

predictors. When Levene's test indicated heterogeneous variance (true for k), data were log-

transformed, which stabilized variance. Normal distribution of residuals was assessed visually.

Lastly, in order to assess the applicability of the TBI approach in tidal wetlands, we

265   separately investigated the temperature response of k and S for the ten sites situated along the North

American Atlantic coast (Fig. 3). Previous studies have shown clear temperature/latitudinal effects

on decomposition and microbial activity along this well-studied transect (Kirwan et al. 2014;

Mozdzer et al. 2014), allowing us to compare the TBI approach with other methods. Regional-scale

transects with sufficient temperature/latitudinal range along other coastlines could not be identified

270 (Fig. 1; Table 1). Statistical analyses were conducted using STATISTICA 10 (StatSoft Inc., Tulsa,

  OK, USA).

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3   Results

3.1   Temperature effects

We found no relationship between temperature and k across study sites (Fig. 2a; Table 2). Also, CART revealed temperature only as a subordinate splitting variable for k. Specifically, temperature seems to positively affect k in meso-tidal systems only (amplitude >2.1m) with sites ≥14.5°C during deployment supporting higher rates of decomposition than sites characterized by lower temperatures. However, this apparent temperature effect was inconsistent within the group of observations with tidal amplitude >2.1m (Fig. S1a). In contrast to the results of the global-scale assessment, k was strongly and positively related with temperature across the ten sites situated along the North American Atlantic coast, with temperature explaining approx. 70% of variability in k (Fig. 3a).

Stabilization was strongly affected by temperature (Fig. 2b; Table 2). The significant negative correlation between S and temperature (Fig. 2b; Table 2) agrees well with the CART. However, CART also identified a narrow temperature range (21.9-23.6°C) in which increasing temperature led to higher stabilization (Fig. S1b; node 11). This group of observations diverging from the general pattern is also clearly visible in Figure 2b and represents the four Mediterranean sites (Ebro Delta and Venice Lagoon) of our survey. The positive relationship between temperature and S was even clearer when focusing on the ten sites along the North American Atlantic coast, with temperature explaining >85% of variability in S (Fig. 3b).

Temperature was highly correlated with latitude and tidal amplitude, and temperature was not independent of soil type (mineral/organic) and ecosystem type (marsh/mangrove) (Table 2). The effect of latitude was similarly pronounced as the temperature effect on S – and consequently – effects of these two parameters on S cannot be separated (Table 2). By contrast, tidal amplitude and soil type did not significantly affect S, and the difference in S between mangroves and marshes was

only marginally significant (Table 2). These findings suggest that the presented temperature effect

320   on S occurs to be mainly independent of tidal amplitude and soil type.

3.2   Effects of relative sea level and nutrient enrichment

Paired comparisons of high vs. low elevated zones indicate no consistent effect of relative sea level

on k across sites ($p > 0.1$; Fig. 4a), whereas S was significantly reduced by 29% in low compared to

325   high elevated zones ($p < 0.01$; Fig. 4b). Testing for effects of relative sea level within each site

separately revealed that S is significantly reduced by 28-87% in the lower elevated zone in 14 of 20

sites; whereas a significant increase of S in low vs. high elevated zones was found in none of the 20

sites (Table S2). This finding demonstrates the consistency of the sea-level effect on S irrespective

of ecosystem type (marsh/mangrove), soil type (mineral/organic), and site salinity (brackish/salt). In

330   nine of the sites, we also found a significant effect of relative sea level on k. However, in six sites k

was significantly higher in low vs. high zones, and in three sites k was significantly lower in low vs.

high zones. The direction of effects on k seems to be independent of ecosystem type, soil type, and

site salinity (Table S2).

The nutrient enrichment treatment at the TIDE project site decreased S by 72% in the high

335   marsh (Fig. 4d). S in the low marsh likewise was similarly low as in the enriched high marsh and

not further reduced by nutrient enrichment (Fig. 4d). In contrast, k was not responsive to the nutrient

enrichment treatment in neither low nor high marsh (Fig. 4c).

3.4   Other factors influencing decomposition rate and stabilization

340   CART revealed tidal amplitude as an important predictor for k. However, this result needs to be

considered cautiously because splits based on tidal amplitude suggest mixed effects (Fig. S1a).

Accordingly, no significant relationship existed between tidal amplitude and k across sites (Table

2). Soil type (mineral/organic) and ecosystem type (marsh/mangrove) did not affect k and S across

sites (Table 2). We found no significant relationship between salinity class and k or S (Table 2).

345   Also, CART did not reveal salinity class as an important factor for k and S.

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4   Discussion

4.1   Temperature effects on decomposition processes

A positive relationship between temperature and decomposition rate was found only at the regional

scale across the ten sites along the North American Atlantic coast (Fig. 3a), but not across all sites

at the global scale (Fig. 2). Even though this finding occurs surprising in the context of basic

biokinetic theory, it is in agreement with findings of Djukic and others (2018), demonstrating

climate effects on the break-down of the TBI materials across terrestrial ecosystems at the biome

scale, but not at the global scale across biomes.

The present study used air temperature as a proxy for top-soil temperature. Thus, the

temperature regime of the decomposition environment was only approximated, which certainly

would have weakened a significant relationship between temperature and k. However, following

typical Q10 values for biological systems of 2-3 (Davidson and Janssens, 2006), k should have at

least doubled over the gradient of $\Delta T >15°C$; yet our data do not even show a tendency of an effect

($r_s = 0.02$; Table 2). We therefore propose that other parameters exerted overriding influence on k,

mainly masking temperature effects, and have not been captured by our experimental design. This

notion is in line with the fact that studies conducted at single-marsh to regional scales report

equivocal results on the temperature response of k, ranging from no or moderate (Charles and

Dukes, 2009; Janousek et al., 2017; Kirwan et al., 2014) to strong seasonally-driven temperature

effects with a Q10 >3.4 as found within a single site (Kirwan and Blum, 2011). For instance, large

differences in site elevation and hydrology could have induced high variability in k across sites and

masked potential temperature effects. Indeed, we demonstrate significant but mixed effects of

relative sea level on k for some sites (Table S2); however, we do not have sufficient data on actual

site elevation or hydrology to control for these factors as covariates affecting the temperature effect

on k. Likewise, we do not have data on nutrient availability, plant productivity, or various

anthropogenic impacts that could have exerted strong control over decomposition processes in the

studied sites (Deegan et al., 2012; Keuskamp et al., 2015a; Macreadie et al., 2017; Mueller et al.,
2016).

In contrast to the missing effect of temperature on k, OM stabilization was strongly affected. Overall, S decreased by 75% over our temperature gradient from 10.9 to 28.5°C (Fig. 2b). Thus, we demonstrate a considerable temperature effect on the initial steps of biomass decomposition in tidal wetlands. However, as also demonstrated for k, the temperature effect on S was much clearer at the regional scale when focusing on the sites along the North American Atlantic coast (Fig. 3b), suggesting high variability in S across regions irrespective of the temperature regime. In accordance, we also demonstrate a clear divergence of the four Mediterranean sites from the regression model (Fig. 2), which could be related to differences in precipitation or nutrient availability across study regions. Future experimental work is therefore required in order to further assess the effects of temperature on OM stabilization and to separate temperature from latitudinal and other interacting effects (e.g. as outlined above for k) that are difficult to control for in observational studies.

The temperature effect on the initial steps of biomass decomposition we identified in the present study is not driven by changes in decomposition rate per se, but – more importantly – by affecting the transformation of fresh and rapidly decomposable organic matter into stable compounds, with potentially important implications for carbon sequestration (e.g. Cotrufo et al., 2013). In their global-scale assessment, Chmura et al. (2003) indeed report a negative relationship of soil organic C density and mean annual temperature within both salt marshes and mangroves. Chmura and colleagues hypothesized stimulated microbial decomposition at higher temperatures to be the responsible driver of this relationship. Plant production and thus OM input is known to increase with latitude and temperature in tidal wetlands (Baldwin et al., 2014; Charles and Dukes, 2009; Gedan and Bertness, 2009; Kirwan et al., 2009), but this increase seems to be more than compensated by higher microbial decomposition. Working at the same spatial scale as Chmura et al.

(2003), our study supports this hypothesis and provides mechanistic insight into the temperature

420   control of OM decomposition as a potential driver of carbon sequestration in tidal wetlands.

4.2   Relative-sea-level effects on decomposition processes

Flooding and thus progressively lower oxygen availability in soil is supposed to be a strong

suppressor of decomposition (Davidson and Janssens, 2006). In tidal wetlands, differences in

425   flooding frequency along elevational gradients often induce sharp gradients in oxygen availability

and redox conditions (Davy et al., 2011; Kirwan et al., 2013; Langley et al., 2013), with potentially

strong influence on OM decomposition and carbon cycling. However, the effect of redox conditions

on OM break-down is determined by the chemical quality of the decomposing material:

Decomposition of aged or recalcitrant OM can indeed be slower and incomplete in the absence of

430   oxygen, whereas the break-down of fresh and labile OM can be largely unaffected by oxygen

availability (Benner et al., 1984; Kristensen et al., 1995). Thus, also decomposition rate and

stabilization of labile, hydrolyzable OM, as assessed in the present study, is not necessarily affected

by redox conditions. Here, we demonstrate that k is not reduced in low (more frequently flooded)

vs. high elevated (less frequently flooded) zones of tidal wetlands (Fig. 4a). This finding is in

435   accordance with an increasing number of studies demonstrating negligible direct effects of sea level

on decomposition rate in tidal wetland soils (Janousek et al., 2017; Kirwan et al., 2013; Mueller et

al., 2016). Furthermore, we show that S is strongly reduced in low vs. high elevation zones,

suggesting that the conversion of recent OM inputs to stable compounds is in fact lower in more

flooded zones of tidal wetlands. As the stabilization of labile OM inputs is a major driver of SOM

440   formation (Cotrufo et al., 2013, 2015; Haddix et al., 2016), one important implication of this finding

is that accelerated SLR yields the potential to decrease the carbon-sequestration potential of tidal

wetlands.

The mechanism by which S is decreased in the more flooded zones of the present study is unknown. Because we did not observe consistent salinity effects on S and k in our data, we do not

445   suppose that regular exposure of litter to salt water explains the unexpected finding. Likewise, soil temperature was not consistently affected by relative elevation across sites ($p > 0.3$; paired t-test based on data shown in Fig. S2). Instead, we argue that more favorable soil moisture conditions in low vs. high elevated zones could have decreased OM stabilization if higher flooding frequencies did not induce redox conditions low enough to suppress microbial activity in the top soil. In support

450   of this, flooding-frequency induced changes in moisture conditions have been reported as primary driver of surface litter break-down, leading to more than four-fold increased litter mass loss in low vs. high marsh zones of a New Jersey salt marsh (Halupa and Howes, 1995). Additionally, greater nutrient availability and less nutrient-limited microbial communities in more frequently flooded zones could have contributed to this effect (Deegan et al., 2012; Kirwan et al., 2013). Strong effects

455   of both high quality marine-derived OM and nutrient amendments on microbial structure and activity have been reported (Deegan et al., 2012; Kearns et al., 2016; Keuskamp et al., 2015b; Mueller et al., 2017), suggesting that regular marine OM and nutrient inputs in more frequently flooded zones can positively affect decomposition (see further discussed below in 4.3).

460   *4.3   Nutrient enrichment reduces stabilization – insights from the TIDE project*
In addition to our global survey of early-stage decomposition processes in tidal wetlands, we included the long-term ecological research site of the TIDE project in Massachusetts, US to experimentally assess both the effects of coastal eutrophication and the relevance of nutrient delivery through floodwater for OM decomposition in tidal wetlands. Important for our argument

465   that decomposition may be favored by higher nutrient availability in low elevated, more frequently flooded zones, we observed a strong reduction (>70%) of S by nutrient enrichment in the high marsh, whereas S in the low marsh likewise was low as in the fertilized high marsh and not further

reduced by fertilization (Fig. 4d). Johnson et al. (2016) demonstrate that nutrient enriched high-marsh plots of the TIDE project receive 19 ± 2 g N m^{-2} yr^1, approximately 10-times the N load of reference high-marsh plots (2 ± 1 g N m^{-2} yr^{-1}; mean$\pm$SE), thus explaining the strong treatment effect observed in the high marsh. In accordance with low stabilization in the reference low marsh, which is equally low as the nutrient enriched high marsh, reference plots of the low marsh receive 16 ± 4 g N m^{-2} yr^1, the same high N load as the enriched high-marsh plots. Surprisingly, however, N loads of 171 ± 19 g N m^{-2} yr^1 in the enriched low-marsh plots do not result in additional reduction of *S* compared to the reference low marsh (Fig. 4d). These findings suggest that microbial communities of the high marsh are N limited, and that N additions to a certain level can stimulate early OM decomposition and thus reduce stabilization. The missing effect of N loads exceeding 16 g m^{-2} yr^1 on stabilization in the low marsh indicates that microbial communities are less or not N limited due to the naturally greater nutrient availability. The findings of the TIDE project therefore support our concept that higher nutrient availability and less nutrient-limited microbial communities in more frequently flooded zones could have contributed to the observed reduction of OM stabilization in low vs. high elevated zones of tidal wetlands in our global assessment.

Although our conclusions on effects of nutrient enrichment on OM decomposition are based on the findings of a single field experiment only, our study adds to a growing number of reports illustrating the impact of coastal eutrophication on tidal wetland C cycling (Deegan et al., 2012; Keuskamp et al., 2015a; Kirwan and Megonigal, 2013; Morris and Bradley, 1999). At the same time, however, we highlight the need to improve our understanding of coastal eutrophication in interaction with other global changes, particularly accelerated SLR and concomitant changes in flooding frequency, on the cycling of both labile and refractory C pools in order to predict future stability of tidal wetlands.

4.4   The Tea Bag Index – methodological considerations

Interpretation of results obtained from standardized approaches like the present needs to be made cautiously because OM quality (i.e. its chemical composition) is a key parameter affecting its

495   decomposition. As the quality of the TBI materials differ from that of wetland plant litters, and likely even more from the quality of the imported allochthonous OM (Khan et al., 2011), we did not expect to capture actual rates of early-stage OM break-down in this study. Instead, we used the TBI to characterize the decomposition environment by obtaining a measure for the potential to decompose and stabilize the deployed standardized material. Standardized approaches like this, or

500   also the cotton-strip assay (e.g. Latter and Walton, 1988), are useful to separate the effects of environmental factors other than OM quality on decomposition processes and to assess their relative importance. Otherwise, complex interaction effects of the abiotic environment and OM quality make it difficult to predict the relevance of certain environmental factors for decomposition processes, potentially masking the effects of important global-change drivers (Prescott, 2010). At

505   the same time, however, the global-change factors considered in the present study are likely to induce changes in the quality of the OM accumulating in tidal wetlands, for instance through shifts in plant-species composition and plant-tissue quality, that can potentially counterbalance or amplify the effects on decomposition processes suggested here. Future research therefore needs to address OM quality feedbacks on decomposition processes in tidal wetlands in order to gain a more

510   complete understanding of global-change effects on tidal-wetland stability and carbon-sequestration capacity.

Based on the S values obtained from initial calculations using the hydrolyzable fractions suggested by Keuskamp et al. (2013), a large number of observations yielded a negative S (Table S3). S becomes negative when the mass loss from green tea is greater than the predicated maximum

515   loss based on its hydrolyzable fraction. At least two processes could have caused this result: First, our data indicate that redox conditions in the top soil of tidal wetlands are not low enough to hamper decomposition of the hydrolyzable fraction of the TBI materials. As a consequence, high

top-soil moisture of tidal wetlands could provide favorable conditions for decomposition, following

typical moisture-decomposition relationships as demonstrated for terrestrial ecosystems (e.g. Curiel

520 Yuste et al., 2007). Potentially, moisture conditions and nutrient supply even allow for considerable

break-down of non-hydrolyzable compounds within three months of deployment, such as lignin

(Berg and McClaugherty, 2014; Duboc et al., 2014; Feng et al., 2010; Knorr et al., 2005). Second,

different protocols to determine the hydrolyzable fraction of plant materials exist and lead to

variable results. The hydrolyzable fraction can consequently be over- or underestimated depending

525 on protocol and type of sample material. The use of the slightly higher hydrolyzable fractions we

determined for calculations of the TBI parameters effectively eliminated negative S values. In that

regard, using the values obtained from the alternative protocol given in Ryan et al. (1990) seemed

more reasonable in our study. However, it needs to be stressed here that direction and size of

reported effects on S and k in the present study are almost independent of the hydrolyzable fraction

530 used for calculations.

Future research will have to test the applicability of the TBI approach in different

ecosystems and test the validity of its assumptions (i.e. S is equal for both types of material used,

and mass loss of non-hydrolyzable material is negligible over 3 months of deployment). The results

of our regional scale assessment along the North American Atlantic coast transect are in tight

535 agreement with previously reported results on cellulose break-down and soil microbial activity

along this well studied transect (Kirwan et al., 2014; Mozdzer et al., 2014). We can thereby

demonstrate the usefulness of the TBI approach to assess early-stage decomposition in tidal-wetland

soils.

540 *4.5   Implications*

This study addresses the influence of temperature, relative sea level, and coastal eutrophication on

the initial transformation of biomass to SOM, and it does not encompass their effects on the existing

SOM pool. However, aspects of S and k are key components of many tidal wetland resiliency models (Schile et al., 2014; Swanson et al., 2014) that have highlighted the critical role of the

545 organic contribution to marsh elevation gain. Although actual rates of S and k cannot be inferred from this study using a standardized approach, our data identify strong negative effects of temperature, relative sea level, and coastal eutrophication on the stabilization of fresh organic inputs to tidal-wetland soils. We argue that these unanticipated combined effects yield the potential to strongly accelerate carbon turnover in tidal wetlands, thus increasing their vulnerability to

550 accelerated SLR, and we highlight the need for experimental studies assessing the extent to which the here identified effects translate into native OM dynamics.

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Author contributions

PM, SN, KJ, and LMS-B designed the overall study. PM analyzed and interpreted the data. PM wrote the initial version of the manuscript with regular comments and editing provided by LMS-B, TJM, and SN. PM, LMS-B, TJM, GLC, TD, YK, AVdG, PE, CS, AD'A,CI, ML, UN, BJJ, AHB, SAY, DIM, ZY, and JW designed and conducted the field studies in the respective sites and commented on an earlier version of the manuscript.

585 **Figure captions**

Figure 1 Overview map of study regions. *Notes:* See Table 1 for region and site details.

Figure 2 Site means of decomposition rate **(a)** and stabilization **(b)** versus mean air temperature during deployment period. Regression line illustrates significant relationship between temperature and stabilization (Table 2); regression model with lowest standard error of estimate (SEE) and

590 highest R^2 is shown: $y = -0.27\ln(x) + 0.99$; $R^2 = 0.239$; SEE = 0.131; excluding Mediterranean sites (21.9-23.6°C; n = 4) from the regression yields: $y = -0.344\ln(x) + 1.233$; $R^2 = 0.510$; SEE = 0.101

Figure 3 Site means of decomposition rate **(a)** and stabilization **(b)** versus mean air temperature of the deployment period shown for the ten sites situated along the latitudinal gradient of the North American Atlantic coast; state abbreviations are shown (compare Table 1). Regression lines

595 illustrate significant relationships; regression models with lowest standard error of estimate (SEE) and highest R^2 are shown. Decomposition rate: $y = 0.001x - 0.0091$; $R^2 = 0.692$; SEE = 0.003; stabilization: $y = -0.712\ln(x) + 2.2331$; $R^2 = 0.860$; SEE = 0.070

Figure 4 (a) Decomposition rate and **(b)** stabilization in high and low elevated zones of tidal marsh and mangrove sites (n = 21; compare Tables 1, S1). **(c)** Decomposition rate and **(d)** stabilization in

600 nutrient enriched versus reference high marsh (*Spartina patens* zone) and low marsh (*Spartina alterniflora* zone) of the TIDE project site at the Plum Island Sound Estuary, Massachusetts, US. Shown are means ± SE and results of paired t-tests (panels a + b) and two-way ANOVAs plus Tukey's HSD test for pairwise comparisons (panels c + d): ns = not significant; * = $p \leq 0.05$; ** = $p \leq 0.01$

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Figure 1

Figure 2
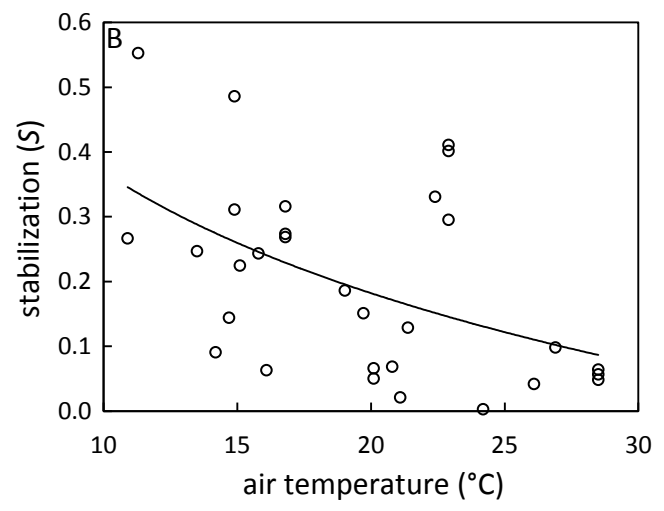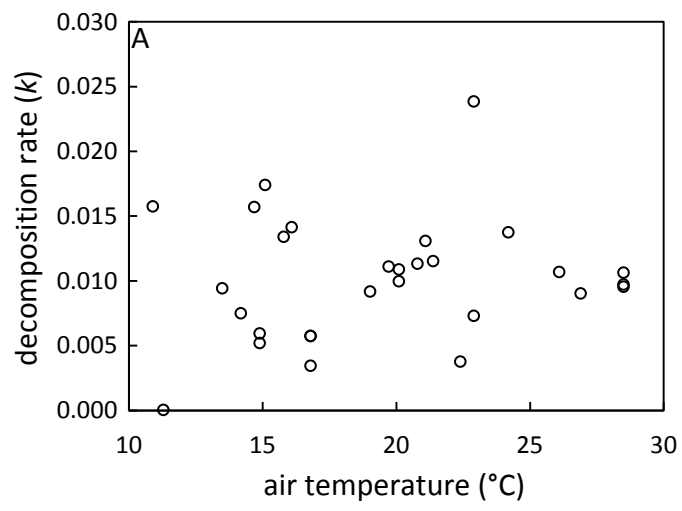
Figure 3
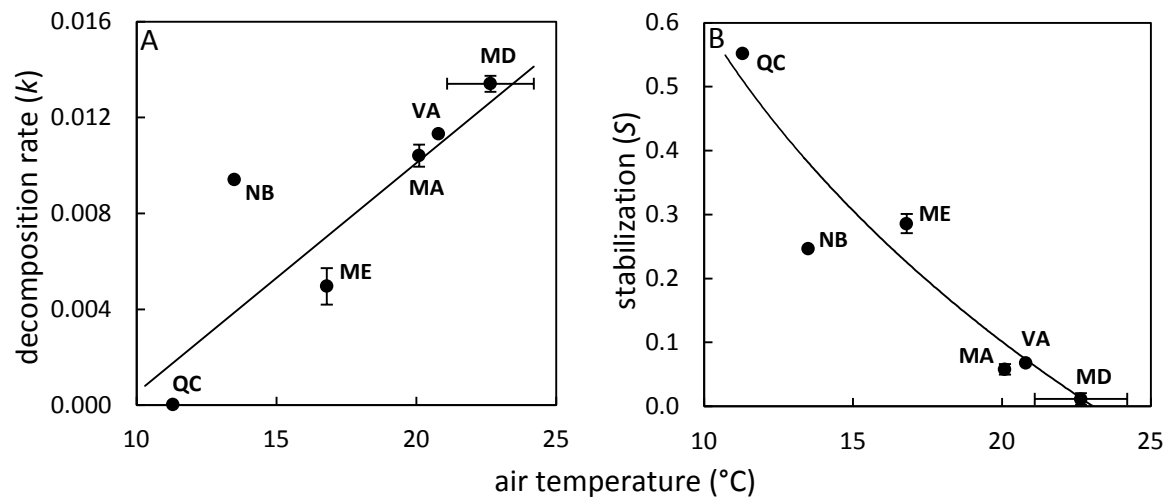
Figure 4
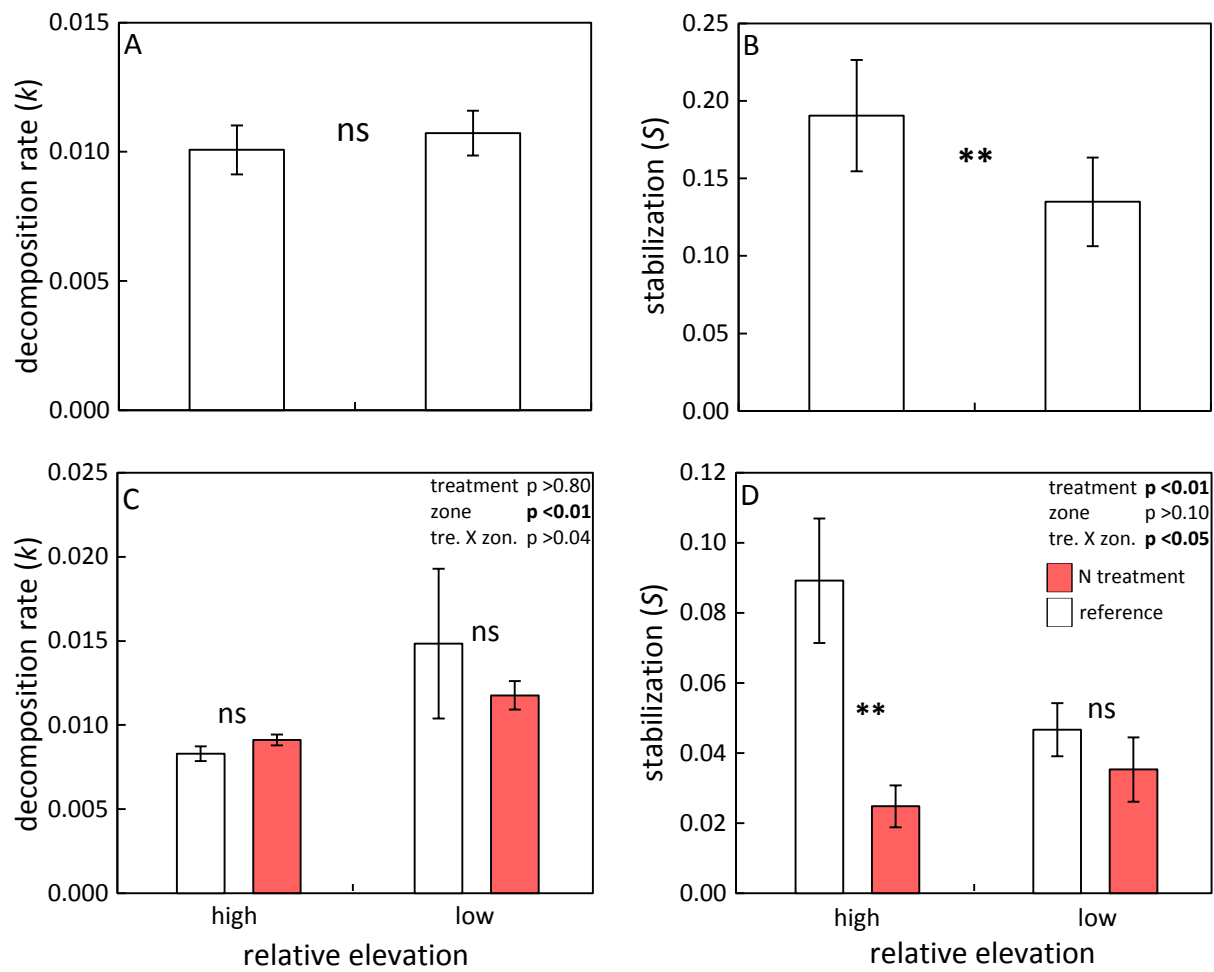
Table 1 Overview of study regions, site names, and site properties. Sites in which tea bags were deployed in zones of different elevation and flooding frequency are marked (x). Different salinity classes are indicated as 'S' (salt water), 'B' (brackish water), and 'F' (fresh water). Tidal amplitude (Ampl.) is given in meters.

Region	Site name	Zonation	Salinity	Ampl.	Ecosystem	Soil[c]	Contact[site ref.]
Europe							
Germany, Wadden Sea	Dieksanderkoog	x	S	3.0	marsh	mineral	Mueller[1]
	Sönke-Nissen-Koog	x	S	3.4	marsh	mineral	Mueller[1]
	Spiekeroog	x	S	2.0	marsh	mineral	Dinter[2]
The Netherlands, Wadden Sea	Ameland	x	S	2.3	marsh	mineral	de Groot[3]
	Noord-Friesland Buitendijks	x	S	2.3	marsh	mineral	Esselink[4]
	Schiermonnikoog[b]	-	S	2.3	marsh	mineral	Smit[5]
Italy, Venice Lagoon	Venice Lagoon	x	S	0.5	marsh	mineral	D'Alpaos[6]
Spain, Ebro Delta	Vilacoto	-	F	<0.1	marsh	organic	Ibáñez[7]
	Garxal	-	B	0.2	marsh	organic	Ibáñez[7]
	Alfacs	-	S	0.2	marsh	organic	Ibáñez[7]
Poland, Gdańsk Bay	Mechelińskie Łąki[b]	-	B	<0.1	marsh	organic	Lazarus
North America							
Canada, St. Lawrence Est., QC	Rimouski	x	S	3.2	marsh	mineral	Neumeier[8]
Canada, Bay of Fundy, NB	Dipper Harbour	x	S	>6.0	marsh	mineral	Chmura[9]
United States, Casco Bay, ME	Long Marsh, north of inlet	-	F	1.4	marsh	organic	Johnson[10]
	Long Marsh, south of inlet	-	B	1.4	marsh	organic	Johnson[10]
	Long Marsh, south of Narrows	-	S	1.4	marsh	organic	Johnson[10]
United States, Plum Isl. Sound, MA	Laws Point	x	S	2.9	marsh	organic	Mozdzer[11]
	TIDE project[a]	x	S	2.9	marsh	organic	Mozdzer[12]
United States, Chesapeake Bay, MD	Patuxent River	x	F	0.7	marsh	organic	Baldwin[13]
	Rhode River	x	B	0.2	marsh	organic	Schile-Beers[14]
United States, Eastern Shore of VA	Wachapreague	x	S	0.6	marsh	mineral	Schile-Beers[15]
United States, San Francisco Bay, CA	Coon Island	x	B	0.7	marsh	mineral	Schile-Beers[15]
	Rush Ranch	x	B	0.7	marsh	mineral	Schile-Beers[15]
	China Camp	-	S	0.7	marsh	mineral	Schile-Beers[15]
Central America							
Belize, Caribbean coast	Twin Cays	x	S	0.2	mangrove	organic	Schile-Beers[16]
Panama, Caribbean coast, Bocas del Toro	Isla Solarte	x	S	0.3	mangrove	organic	Schile-Beers[17]
	Isla Cristóbal	x	S	0.3	mangrove	organic	Schile-Beers[17]
	Isla Popa	x	S	0.3	mangrove	organic	Schile-Beers[17]
South America							
Argentina, Mar Chiquita Lagoon	Mar Chiquita[b]	x	B	0.8	marsh	mineral	Montemayor[18]
Asia							
China, Yangtze Estuary	Dongtan	x	S	2.5	marsh	mineral	Wu[19]

Notes: (a) additional fertilization treatment was included, compare reference 10; (b) low retrieval rates of paired bags only allowed for calculation of site or zone averages (c) If unclear, soil type was judged as mineral at organic matter contents < 35% (Soil Survey Staff, 2014); Site references: (1) Nolte et al. (2013), (2) Flemming and Davis (1994), (3) Dijkema et al. (2010), (4) Chang et al. (2016), (5) Howison et al. (2015), (6) Roner et al. (2016), (7) Benito et al. (2014), (8) Neumeier and Cheng (2015), (9) (Chmura et al. (1997), (10) Craig (2015), (11) Morris et al. (2013), (12) Deegan et al. (2012), (13) Neff et al. (2009), (14) Langley and Megonigal (2010), (15) Vasey et al. (2012), (16) Mckee et al. (2007), (17) Lovelock et al. (2005), (18) Isacch et al. (2006), (19) Yang et al. (2017)

Table 2 Spearman rank coefficients between the variables temperature, latitude, tidal amplitude, salinity class, k, and S (coefficients are bold typed at p ≤ 0.05) and comparisons of temperature (°C), latitude (°), amplitude (m), k, and S between ecosystem types (mangrove vs. marsh) and soil types (mineral vs. organic) shown as site means ± SE, n = 30. Asterisks show results of Mann-Whitney U tests and denote significant differences as: p ≤ 0.1 = ˙, p ≤ 0.05 = *, p ≤ 0.01 = **, not significant = ns.

	temperature	latitude	amplitude	salinity	S	k
Spearman rank correlations						
temperature		**-0.78**	**-0.68**	-0.09	**-0.44**	0.02
latitude	**-0.78**		**0.49**	0.05	**0.43**	0.06
amplitude	**-0.68**	**0.49**		**0.40**	0.01	0.00
salinity	-0.09	0.05	**0.40**		-0.13	-0.08
S	**-0.44**	**0.43**	0.01	-0.13		**-0.51**
k	0.02	0.06	0.00	-0.08	**-0.51**	
group means ± SE						
soil type	**	ns	**		ns	ns
mineral	17.0±1.1	45.5±2.1	2.3±0.6		0.22±0.04	0.010±0.001
organic	22.2±1.2	34.5±3.9	0.8±0.3		0.17±0.04	0.010±0.001
ecosystem	**	**	*		˙	ns
marsh	18.3±0.8	44.4±1.3	1.7±0.4		0.22±0.03	0.010±0.001
mangrove	28.1±0.4	11.4±2.0	0.3±0.0		0.07±0.01	0.010±0.000