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Sensitivity of mangrove soil organic matter decay to warming and sea level change

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Abstract

Mangroves are among the world's most carbon-dense ecosystems, but they are threatened by rapid climate change and rising sea levels. The accumulation and decomposition of soil organic matter (SOM) are closely tied to mangroves' carbon sink functions and resistance to rising sea levels. However, few studies have investigated the response of mangrove SOM dynamics to likely future environmental conditions. We quantified how mangrove SOM decay is affected by predicted global warming (+4°C), sea level changes (simulated by modification of the inundation duration by zero, two and six hours per day), and their interaction. Whilst changes in inundation duration between two and six hours per day did not affect SOM decay, the treatment without inundation led to a 60% increase. A warming of 4°C caused SOM decay to increase by 21%, but longer inundation moderated this temperature-driven increase. Our results suggest that i) sea level rise is unlikely to decrease the SOM decay rate, suggesting that previous mangrove elevation gain, which has allowed mangroves to persist in areas of sea level rise, might result from changes in root production and/or mineral sedimentation; ii) sea level fall events, predicted to double in frequency and area, will cause periods of intensified SOM decay; iii) changing tidal regimes in mangroves due to sea level rise might attenuate increases in SOM decay caused by global warming. Our results have important implications for forecasting mangrove carbon dynamics and the persistence of mangroves and other coastal wetlands under future scenarios of climate change.

Introduction

Mangroves are among the most carbon dense ecosystems in the world (Donato et al., 2011), and provide ecosystem services worth US$194,000 per hectare per year (Costanza et al., 2014). The conservation and restoration of mangroves are increasingly being promoted (Lee et al., 2019; McLeod et al., 2011). Several countries have already committed to using coastal wetlands as part of their mitigation and adaptation strategies for climate change (Herr et al., 2015) and re-forestation and conservation projects are taking place widely (Lee et al., 2019). In Bangladesh and Vietnam, for example, more than 200,000 ha of damaged or destroyed mangroves have been replanted in the last 50 years. However, against a backdrop of changing future climates it is unclear whether natural and restored mangroves will be resilient to sea level rise, and in particular whether they will continue to sequester soil carbon (Gilman et al., 2008; Lovelock et al., 2015).

The accumulation of soil organic matter (SOM) controls both the carbon sink capacity of mangroves and their resistance to sea level rise (Alongi, 2009; Rogers et al., 2019). In carbon-dense mangroves such as our study site (see next section), SOM accumulation results primarily from the balance between organic matter decay and root production (Alongi, 2009; Middleton and McKee 2001; Bouillon et al. 2003). Since SOM represents up to 80% of the carbon stored in mangroves (Alongi, 2009), the alteration of SOM decay by climate change is likely to affect their carbon sink capacity in the future. Accumulation of SOM in mangroves causes the soil surface to rise within the tidal prism. If the rate of soil accretion in mangroves equals or is faster than the rate of sea level rise, mangroves can persist and avoid being submerged (Rogers et al., 2019). In contrast, an increase of root decay might reduce or even reverse SOM accumulation, leading to subsidence, thus causing relative sea levels to rise. Temperature and inundation regimes are major factors controlling SOM decay in mangroves, and will be modified by climate and sea level change (Alongi, 2009; Kristensen et al., 2008; Lovelock, 2008); Yet, compared to many others ecosystems, little is known about how mangrove SOM dynamics will respond to future environmental conditions (Jennerjahn et al., 2017; Song et al., 2019; Twilley et al., 2017).

Global mean temperature is expected to rise between 1.0 and 4.8°C by 2100 under RCP2.6 and RCP8.5, respectively, relative to the 1986–2005 baseline (IPCC, 2013). Rising temperatures have been shown to increase rates of SOM decay in coastal wetlands (Kirwan et al., 2014; Morris & Whiting, 1986), but only a few mangrove sites have been investigated. Field studies have used latitudinal gradients to infer the thermal sensitivity of mangrove SOM decay, and therefore incorporate site-specific confounding factors such as tidal inundation regime, root respiration, biofilm development, and soil nutrient status (Lovelock, 2008; Jin et al., 2013; Lewis et al., 2014; Poungparn et al., 2009). Since it is challenging to isolate the effect of temperature in the field, a more controlled laboratory approach is necessary (Lovelock, 2008; Twilley et al., 2017).

Global sea level is projected to rise between 0.28 and 0.98 m by 2100 (RCP2.6 and RCP8.5, respectively, relative to the 1986–2005 baseline, IPCC, 2013) and incidences of extreme sea levels are expected to become more frequent (IPCC, 2013), yet the impacts of these changes upon SOM decay in mangrove soils are understudied. As sea level rises, mangroves can migrate landward or can accumulate organic matter and sediments. Through these mechanisms mangroves can occupy landward and vertical 'accommodation space' (Rogers et al., 2019). In the past, some mangroves have adjusted to sea level rise and avoided submergence by accreting soil, notably SOM (McKee et al., 2007; Krauss et al. 2014). However, it is unclear whether the vertical accretion of mangrove soil (where it occurs) is driven primarily by an increase of root production and sedimentation, reduced SOM decay rates, or both. Landward accommodation space for mangroves is limited in many countries due to coastal urbanisation; while vertical soil elevation may be limited by a lack of riverine sediment inputs to the coast (Lovelock et al., 2015; Schuerch et al., 2018). Some mangroves therefore seem likely to experience an increasing duration of tidal inundation, or will become fully submerged with continued sea level rise (Lovelock et al., 2015; Ward et al., 2016).

There is a dominant view that increased flooding is inversely related to decomposition rate in coastal wetlands (Davidson & Janssens, 2006; Nyman & DeLaune, 1991; Reed, 1995; Miller et al., 2001), but there is a surprising lack of empirical data that may be used to test such a hypothesis (Mueller et al., 2016), particularly for mangroves. In some settings, mangroves will experience prolonged and repeated sea-level drops, for up to a year (Widlansky et al., 2015). These incidences of extreme sea levels, known as Taimasa, lower the sea level by as much as 0.30 m and reduce the inundation of inter-tidal mangrove habitats (Widlansky et al., 2015). Taimasa events have already been shown to contribute to drought conditions in mangroves, resulting in large areas of mangrove dieback (Lovelock et al., 2017). Taimasa events are predicted to become more intense and frequent with future climate change, even against a long-term backdrop of rising relative sea level (Widlansky et al., 2015). However, the impacts of Taimasa events or other types of drought (e.g., those caused by reductions in riverine flows into coastal water) on SOM decay in mangroves remain unexplored (Chapman et al., 2019).

Here, we conducted a fully factorial mesocosm experiment to reveal the direction and magnitude of change in mangrove SOM decay rate in response to important global environmental changes. We posed the following research questions:

i) How much will rates of SOM decay increase with global warming?

ii) How will changes in inundation associated with Taimasa events and sea level rise affect rates of SOM decay?

iii) How will SOM decay rates respond to the combined impact of increases in temperature and changes in inundation?

Methodology

Experimental design and setup

We conducted an incubation experiment to simulate how warming and relative sea level change might affect SOM decay rates in mangrove soil. We used CO_2 efflux from the mesocosms as a proxy for rates of SOM decay. The mesocosm approach allowed us to limit confounding factors, while revealing the independent effect sizes of temperature and inundation, as well as their interaction. We incubated samples for 22 days at two temperatures (27°C and 31°C) and under three inundation regimes (zero, two and six hours of inundation per day). Those factors were combined factorially and resulted in six treatments in total. The 4°C difference between our two temperature treatments is within the range of surface warming predicted for 2100 under RCP8.5, both globally (RCP8.5- IPCC, 2013; Ward et al., 2016), and locally at our study site in the Mekong Delta, Vietnam (MONROE, 2009; Katzfey et al., 2014) (see below). The six-hour inundation treatment represents an increase of inundation duration due to sea level rise; the two-hour treatment is the baseline condition; while the zero hour inundation treatment represents a drought event, such as that caused by falling sea level during a Taimasa event. Likely impacts of sea level change on the duration of inundation in mangroves have not yet been established due to a lack of understanding of soil surface rise in response to SOM inputs in these ecosystems, so we took a simplified approach. We chose two hours of inundation as our baseline condition because the mangrove trees (from the genus *Rhizophora*) found at our site are inundated for a minimum of two hours per day (van Loon et al., 2007). We chose the six hour treatment to represent the longest duration of inundation that can be found for the genus *Rhizophora* at our study site (van Loon et al., 2007), and because the difference in altitude between these durations of approximately 60 cm (van Loon et al., 2007) corresponds to the projected sea level rise in the Mekong Delta region (MONROE, 2009).

For each of our six treatments, we had ten replicate mesocosms, each of which we sampled five times during the course of the experiment, for a total of 300 CO_2 efflux measurements. The mesocosms were constructed from PVC tubes 11 cm long and 6 cm in diameter, drilled at their top to allow lateral exchange of water into and out of the mesocosm. Each mesocosm was filled with 330 grams of wet soil to a height of 7 cm, and packed to match field bulk density as closely as possible. We homogenised the soil and removed any large pieces of organic matter (> 5 mm). At the bottom of each mesocosm, we installed a mesh screen to allow the vertical exchange of water. We controlled temperature with two environmental chambers set to a constant temperature of 27 and 31°C. The soil samples were placed in tanks in which the inundation regimes were controlled in two ways. Flood tides were created by pumping water gradually into the tanks using a peristaltic pump, and the ebb tide simulated by gradually reducing the water level with a flush mechanism activated by an automatic arm. Both flood and ebb were programmed using a Python script and a Raspberry Pi microcomputer. The soil samples were placed at different levels in the tanks to give the different inundation treatments. The two- and six-hour treatments were kept inundated for the whole two or six hours. The inundation depth was two cm in the mesocosm inundated two hours, and ranged from two to four centimetres for the mesocosm inundated for six hours (four hours at two centimetres and two hours at four centimetres). We used artificial sea water, prepared by mixing Instant Ocean® with distilled water to prevent any additional input of organic matter that could have potentially been added by using in-situ sea water (Lewis et al., 2014). The salinity of the artificial seawater was 30 ppt, which is within the range of the salinity in our field site (Dung & Duc, 2016) and in mangrove tidal water more generally (Chen et al., 2014; Frusher et al., 1994; Lara & Cohen, 2006; Marchand et al., 2004). The bases of the mesocosms in the zero-hour treatment (< 5 mm) were wetted daily for two hours to prevent any gas loss during flux measurement (see below). We conducted the experiment in an environmental room with no natural or artificial light to inhibit any photosynthetic activity.

Field study site description and sample collection

The soil for the experiment was collected in the mangroves of Can Gio, located in the north of the Mekong Delta, Vietnam (10°30′ N, 106°52′ E). The tidal regime of Can Gio is semi-diurnal. The frequency with which mangroves are inundated ranges from twice per month to twice per day (van Loon et al. 2007). The mangroves of Can Gio occupy an area that extends from below the mean sea level to more than two meters above it. Organic carbon content, sediment particle size distribution and nutrient concentrations of the soil used in the experiments were comparable to other carbon rich mangroves (Table 1). The organic matter content of the soil, estimated by loss on ignition, was 10.5% of the bulk soil weight, which is similar to that found in the most carbon-rich deltaic mangroves in the Indo-Pacific region (Donato et al., 2011). Grain size distribution of our samples was dominated by clay and silt, which is also typical for deltaic mangroves (Table 1). Soil nutrient content was 0.39% N and 0.03% P of bulk dry weight. After forest destruction caused by the war between the USA and Vietnam, the area was replanted in 1986 with *Rhizophora apiculate* Blume, a common species used in mangrove rehabilitation projects in the Mekong Delta and elsewhere. Soil sampling from three sites took place in February 2018. After removing the surface litter, we collected 14 kg of wet soil from the top soil layer (0-15 cm) at each site. The wet samples were transported to the laboratory and stored at 4°C to limit losses of SOM.

Table 1: Soil characteristics

Grain size distribution (%) [1]		**Nutrient and Carbon (%)**[2]	
Clay	67.01	Total nitrogen	0.39
Silt	32.97	Total phosphorus	0.04
Sand	<0.02	Total organic carbon	10.19

[1] Grain size distribution was measured with a laser diffraction particle size analyser on wet samples treated with hydrogen peroxide.[2] TN and TOC were analysed with an elemental combustion analyser (Vario Micro Cube) after removal of the inorganic carbon with hydrochloric acid, and TN and TP were analysed with a continuous flow autoanalyser (Skalar SAN + + auto analyser). % of the bulk dry weight.

Gas fluxes measurement and calculation

SOM decay was estimated by measuring carbon gas (CO_2 and CH_4) fluxes from the mesocosms using mini flux chambers. After an initial seven-day stabilisation period, we sampled on five occasions: days 1, 2, 5, 9 and 16. The CH_4 fluxes during the experiment were negligible, so we do not consider CH_4 further (Supporting Information 2, Table S1). The gas flux measurements were taken under dark conditions when the soil was not inundated, one to three hours after ebb. Gas concentrations in the mini chambers during flux tests were measured using off-axis integrated cavity output spectroscopy (Los Gatos Research Ultra-portable GHG Analyzer, model 915-0011, California). During the tests, ppmv gas concentrations in the mini flux chambers were measured at 1 Hz. The chambers were sealed to the top of the mesocosm for a total of 150 seconds. During the tests, the temperature and pressure of the environmental chamber in which the mesocosms were housed were recorded (pressure accuracy of ~ ± 0.5 hPa and precision of ~ 0.2 hPa; temperature accuracy of ~ ± 0.5°C and precision of 0.2°C; Commeter C4141 probe: Comet Systems, Rožnov pod Radhoštěm, Czech Republic) to allow calculation of gas fluxes. Before each test, the water-exchange ports (drilled holes) in the sides of the mesocosms were blocked with gas-tight rubber bungs. We also wore a respirator (3 M 7501 Silicone half mask respirator) connected to the outside of the environmental chamber to remove any exhaled CO_2. To calculate the gas fluxes we converted ppmv gas concentrations in the mini flux chambers into masses using the ideal gas equation. Ordinary least squares regression was then used to estimate the rate of change in gas mass over time which could then be converted into a mass flux when the volume of the mini chamber and area of the soil samples were taken into account. Fluxes were calculated only if the slope of the linear regression was i) significantly different from zero ($p < 0.05$), ii) the coefficient of determination (r^2) was > 0.70, and iii) the difference between the minimum and maximum gas concentration were above the error range (7.15 ppmv) of the Los Gatos instrument. In instances where measured concentrations did not satisfy criterion (iii), we recorded a zero flux. In total, 296 fluxes from 300 were valid and used in our statistical analysis.

CO_2 flux as an estimate of SOM decay

CO_2 fluxes from soils are controlled by microbial decomposition of organic matter, autotrophic root respiration, algae, chemolithotrophs and macrofauna (Kuzyakov, 2006; Lovelock, 2008). The largest CO_2 flux is likely to be from microbial decomposition of organic matter, followed by root respiration (Ouyang et al. 2018). Our measurements would have excluded autotrophic root respiration because no living roots were present in them (and larger roots were, anyway, removed – see above, Bloom & Caldwell, 1988). In some mangroves, biofilms have been shown to contribute to soil CO_2 efflux (Jacotot et al., 2019; Lovelock, 2008), although they do not exert any direct control over the decay of SOM itself. Visual checks were carried out before each gas measurement, but no biofilm development was apparent. Macrofauna were excluded when we extracted the soil in situ, and we did not notice any macrofauna when the soil was mixed prior to being put in the mesocosms. Between measurements, the soil was kept in dark conditions to limit any phototrophic respiration. Thus we are confident that our measured CO_2 emissions represent SOM decay alone.

Experimental limitations

Our use of homogenised mangrove soil has reduced the complexity of the soil to avoid confounding factors (e.g., different initial SOM contents, root densities or faunal respiration). For instance, faunal burrowing activities in natural soils might be expected to increase soil aeration and so aerobic respiration; while live fine roots in natural soils might release root exudates. Such factors are likely to exert some influence on SOM decay in coastal wetlands (Kristensen et al. 2008, Mueller et al., 2016) and are also likely to respond to inundation duration and temperature changes. These differences between our soils and natural mangrove soils should be borne in mind when interpreting our results.

Statistical analysis

A linear mixed model was used to investigate how SOM is affected by temperature, inundation and the interaction of temperature and inundation. The reason for using a mixed model is because we took repeated measurements in each soil mesocosm, thereby raising the possibility of a hierarchical structure in our data set. Initial visual inspection of the data clearly indicated that measured rates of CO_2 efflux declined throughout the experiment, meaning that our data exhibited obvious clustering by date of measurement (Supporting Information 1). Such a situation violates the assumption of independence of measurements required by regression analysis and ANOVA, but using a mixed model overcame this problem because it explicitly models the non-independence of our data (Supporting Information 1).

To construct our linear mixed model, we began with a baseline model, and used a forward addition method adding one predictor (fixed or random effects) at a time. Doing so allowed us to assess the effect of each predictor on the overall performance of the model using the Akaike information criterion (AICc) and the likelihood ratio (Zuur et al., 2007; $p < 0.05$ threshold).

We set the day of measurement to be the subject variable, and experimented with a random intercept and random slopes for the effects of temperature and inundation period, that were allowed to vary between measurement days. Doing so accounted for the possibility that measurements were more similar within days than they were between days (i.e., representing any long-term drift in CO_2 efflux during the course of our experiment). All the CO_2 flux data were transformed using a $\log_{10}$ function in order to ensure linear, heteroscedastic fits.

The baseline model consisted solely of a fixed-effect intercept, which is equivalent to the grand mean of the entire dataset. Next we added a random intercept that varies by date of measurement, in order to assess the effect of long-term drift; but no other predictors. The random intercept model is equivalent to a one-way ANOVA that predicts the mean CO_2 efflux across all treatments according to date of measurement. This random intercept led to a significant improvement in model performance (-67 of the AICc, $p < 0.001$), reflecting the important role of date of measurement. We then proceeded to experiment with adding fixed slopes for temperature and inundation regimes, and their interaction; and then random slopes for temperature, inundation and their interaction. Each time we re-specified the model, we re-evaluated its performance compared to the previous iteration to ascertain whether the alteration had significantly improved its fit according to AICc. All models that included random slopes were numerically intractable, and either failed to converge or had singular fits (Supporting Information 1). CO_2 efflux was best described by a model that has fixed effect slopes for temperature, inundation, and their interaction; and the random intercept for date of measurement. Visual inspection of residuals did not reveal any obvious deviations from normality, homoscedasticity or linearity (Supporting Information 1). We used ANOVA to investigate the effect of the main treatments and their interaction on SOM decay (Supporting Information 1), and the least square means with a Tukey's adjustment of *p*-values as a post hoc test to investigate differences between the levels of each factor (Lenth, 2016), including both main effects and interactions. All statistical analyses were performed using r (r core Team, 2013). We built the linear mixed model using the lmer function from the r package lme4 (Bates et al., 2015). AICc was computed using the function AICc from the r package MuMin (Barton, 2019), and least square means were computed with the function lsmeans from the r package lsmeans (Lenth, 2016). Full details of the analysis, the r scripts and our data are provided as Supporting Information 1 to ensure the full reproducibility of our analysis.

Results

The CO_2 efflux data are summarized in Fig. 1. Average CO_2 efflux varied by a factor of two across our treatments, with the highest averages from samples exposed to high temperature and zero hours inundation treatment; and the lowest CO_2 efflux from samples inundated for two hours per day at 27°C (Fig. 1c).

A rise of temperature by 4°C increased mean soil CO_2 efflux by 21 % ($p < 0.001$, $F_{(1,291)} = 27.83$). The inundation regime also affected the mean soil respiration ($p < 0.001$, $F_{(2,291)} = 47.72$). The zero hours inundation treatment emitted 66 % more CO_2 than the two-hour inundation treatment ($p < 0.001$, least square means = 0.168, $t_{(296)} = 8.774$), and 60 % more than the six-hour treatment ($p < 0.001$, least square means = 0.152, $t_{(296)} = 7.931$). In contrast, the CO_2 fluxes from the two-hour and six-hour treatments were not significantly different from one another ($p = 0.691$, least square means = -0.016, $t_{(296)} = -0.820$). Temperature and inundation interacted significantly to affect soil respiration ($p < 0.001$, $F_{(2,291)} = 16.41$). In the samples that were never inundated, the higher-temperature treatment increased CO_2 emissions by 45 % ($p < 0.001$, least square means = 0.201, $t_{(296)} = 7.440$). For the two-hour inundation treatment, the higher-temperature treatment increased soil respiration by 14 %, ($p = 0.039$, least square means = 0.056, $t_{(296)} = 2.070$). For the six-hour inundation treatment there was no effect of warming upon soil respiration ($p = 0.666$, least square means = -0.012, $t_{(296)} = -0.433$). See Fig. 1 and Table 2 and 3 for details.

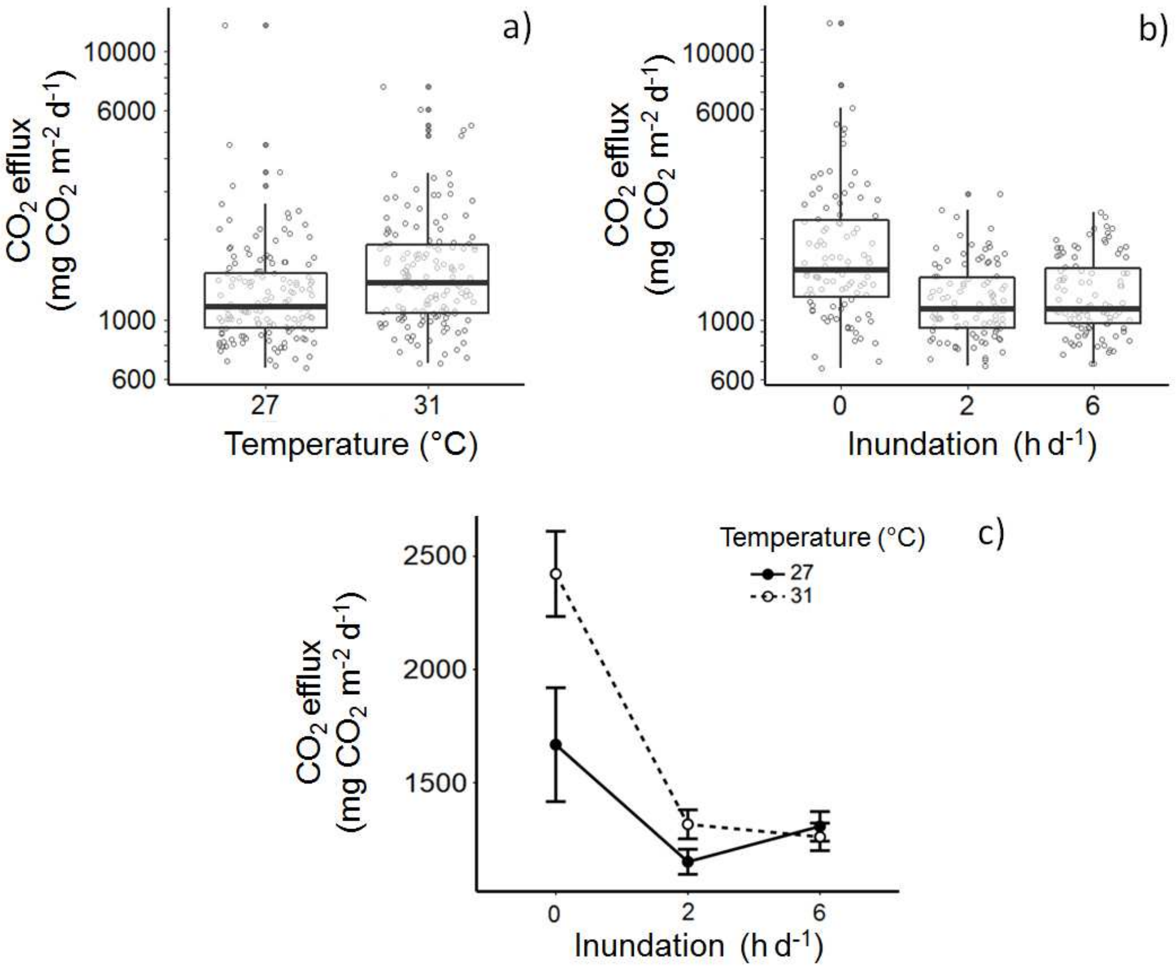

Fig. 1 The response of SOM decay of mangrove (CO_2 efflux) to (a) temperature, (b) inundation regime, and (c) the interaction of temperature and inundation regime. Bold, horizontal lines in (a) and (b) show sample medians. Note logarithmic vertical axis scales in (a) and (b). Symbols in (c) show sample means; error bars show standard errors. For (a), (b) and (c) $n = 296$.

Table 2: Effects of the inundation, temperature and their interaction on the SOM decay rate ($\log_{10}$ CO_2 efflux) using ANOVA. Significant effects ($p < 0.05$ threshold) shown in bold. Dfn and Dfd are degrees of freedom in numerator and denominator, respectively.

Treatments	**Dfn**	**Dfd**	***F*-value**	***p*-value**
Temperature	1	291	27.83	**< 0.001**
Inundation	2	291	47.72	**< 0.001**
Temp:Inundation	2	291	16.41	**< 0.001**

Table 3: Effects of each inundation levels and the temperature treatments with each inundation level on the SOM decay rate ($\log_{10}$ CO_2 efflux) with the least square means as post hoc test for the linear mixed model. Significant effects ($p < 0.05$ threshold) shown in bold.

Treatments		**Estimated marginal means ($\log_{10}$ mg CO_2 m^{-2} d^{-1})**	**Df**	***t*-value**	***p*-value**
0 h - 2 h d^{-1} inundation		0.168	296	8.774	**< 0.001**
0 h - 6 h d^{-1} inundation		0.152	296	7.931	**< 0.001**
2 h - 6 h d^{-1} inundation		-0.016	296	-0.820	0.691
31 - 27° C	**0 h d^{-1} inundation**	0.201	296	7.440	**< 0.001**
	2 h d^{-1} inundation	0.056	296	2.070	**0.039**
	6 h d^{-1} inundation	-0.012	296	-0.433	0.666

Discussion

We reveal the independent effect sizes of temperature and inundation, and their interaction, upon SOM decay rates in mangroves, independently of confounding factors. Our results have a direct relevance to: i) the prediction of soil carbon fate under future environmental conditions; and ii) understanding the likely persistence of mangroves under sea level change and global warming.

Thermal sensitivity of mangrove SOM decay

SOM decay was affected by warming, as has been observed in other coastal wetlands and in some mangroves; however, the thermal sensitivity of the SOM decay determined here was in the lower range of what has been described for mangroves. Other studies have reported an increase in SOM decay ranging between 0 and 100 % with a temperature rise of ~5°C (from 25 to 30°C, Jin et al., 2013; Lewis et al., 2014; Lovelock et al., 2008; Poungparn et al., 2009; Simpson et al., 2019). This large range of SOM thermal sensitivity reported for mangroves is likely attributable to some combination of: i) the inclusion of autotrophic respiration in addition to heterotrophic respiration in field studies (Ouyang et al., 2018); and ii) the assumption that temperature is the dominant control on SOM decay, which our results do not entirely support. In our study, the interaction between temperature and inundation had a significant effect on SOM decay, whereby increasing inundation duration reduced the thermal sensitivity of SOM decay (Fig. 1). A potential explanation for the reduced thermal sensitivity of SOM decay with longer inundation could be that the input of water during inundation reduced the soil temperature in the mesocosms (Dalva & Moore, 1993), but the artificial seawater used to inundate the soils in our experiment was kept at air temperature in each of the environmental chambers; therefore, this is not a plausible explanation here. Rather, we might conjecture that the large effect of temperature in the mesocosms without inundation is likely due to increased soil aeration and drying at 31°C compared to 27°C (based on visual observations). In contrast, the inundated mesocosms (two and six hours per day) might have remained waterlogged between the inundation events due to slow drainage from our fine-grained clay soils (Table 1, Schwendenmann et al. 2006). The low to absent thermal sensitivity of SOM decay in frequently-inundated soil suggests that: i) SOM of low inter-tidal mangroves might be less sensitive to warming induced by climate change; and ii) more general sea level rise is likely to counterbalance the impact of warmer temperatures on SOM decay, at least in part, and provide some protection to mangrove soil carbon stocks under climate change.

Response of SOM decay to an inundation gradient

SOM decay did not decrease monotonically with an increased duration of inundation, as is often assumed in coastal wetlands (Davidson & Janssens, 2006; Nyman & DeLaune, 1991; Reed, 1995; Miller et al., 2001). The SOM decay showed rather a dichotomous response between inundated (the two-hour and six-hour per day treatments) and not-inundated soil (zero-hour per day inundation). The suppression of tidal inundation – a potential consequence of Taimasa or other drought events – caused increases of 66% in CO_2 emissions from the mangrove soil. To our knowledge, no previous studies have looked at the effect of drought on mangrove SOM decay, but studies on tropical forested peatlands have shown similar rises of CO_2 fluxes when artificially drained (e.g., Hooijer et al., 2012). The lowering of the water table in carbon-rich soils induces a shift from anaerobic to aerobic conditions resulting in faster SOM decay (Chapman et al., 2019; Hooijer et al., 2012; Wolf et al., 2007). Taimasa events might therefore represent a major threat to mangrove carbon stocks, since they are projected to double in frequency, and nearly double in the area that they will affect, over the next 100 years (Widlansky et al., 2015).

Our representation of sea level rise, as an increase in inundation duration from two to six hours per day, had no significant effect upon rates of SOM decay, a finding that contrasts with the only two previously reported studies on mangroves, in both of which SOM decay was suppressed by increasing inundation (Lewis et al., 2014; Chambers et al., 2014: see treatment under ambient salinity). The mesocosms that were inundated for two and six hours per day might have remained close to waterlogged between inundation events due to the slow drainage of the fine-grained sediments, which might explain the similar response of soil CO_2 efflux for those two treatments (Schwendenmann et al. 2006). Our results are similar to those reported in many studies on saltmarshes where increases in inundation duration had a limited effect on SOM decay (Kirwan et al., 2013; Hackney, 1987; Blum, 1993; Blum &Christian, 2004). We might conjecture that, like in saltmarshes, the input of saline water during our flooding treatments promoted the decay of SOM through sulfate reduction, and this compensated for the slower decomposition of SOM found normally under anaerobic conditions (Kirwan et al., 2013; Weston et al., 2011). Similar results have been observed by Chambers et al. (2014) in an outdoor mangrove mesocosm experiment that used similar levels of salinity – 15 ppt and 35 ppt – to us. Chambers et al. (2014) found that under low salinity the increased inundation duration resulted in lowering of SOM decay, while under high salinity, the SOM decay was not affected by the inundation duration increase. This suggests that increase of sulfate concentration of the water inundating the soil explains the variability of the SOM decay. Other factors are also likely to have contributed, because the increase of inundation with water of low salinity (< 12 ppt) has previously been shown to have no impact on SOM decay in a saltmarsh (Kirwan et al., 2013). Our results demonstrate that, like in saltmarshes, increased inundation in mangroves does not necessarily lead to a decrease in SOM decay rate. This implies that the persistence of mangroves to sea level rise, by vertical soil building and elevation in the tidal frame, does not exclusively rely on a reduction of SOM decay. Root production or mineral sedimentation are also likely to play a major role and require further investigation. Human impacts on those processes might represent additional threats to mangroves resilience to sea level rise; for instance, multiple river dams trapping sediments and large-scale commercial sand mining decreasing considerably the suspended sediments input to the coasts (Dai et al., 2009; Anthony et al., 2015), are highly likely to compromise the capacity of some mangroves to keep pace with relative sea level rise in the future.

Conclusions

By isolating the effects of temperature and inundation, and also considering them in combination, we reveal that:

1) Rates of SOM decay do not decrease with simulated sea level rise in our experiments. Previous reports of mangroves adapting to sea level rise through increased net SOM accumulation (McKee et al., 2007; Krauss et al. 2014) therefore seem likely to have been the result of an increase in root production rather than a reduction in SOM decay.
2) Drought conditions are likely to sharply raise SOM mineralisation of mangroves, and global warming might exaggerate this effect.
3) Climatic warming is likely to increase SOM decay rates, but the impact of rising temperatures may be lower than previously suspected, especially in mangrove soils that become inundated by rising relative sea levels.

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