Analysis of Organic Matter Decomposition in the Salt Marshes of the Venice Lagoon (Italy) Using Standard Litter Bags

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Abstract

Tidal salt marshes are widespread along the World's coasts, and are ecologically and economically important as they provide several valuable ecosystem services. In particular, their significant primary production, coupled with sustained vertical accretion rates, enables marshes to sequester and store large amounts of organic carbon and makes them one of the most carbon-rich ecosystems on Earth. Organic carbon accumulation results from the balance between inputs, i.e. organic matter produced by local plants or imported, and outputs through decomposition and erosion. Additionally, organic matter deposition actively contributes to marsh vertical accretion, thus critically affecting the resilience of marsh ecosystems to rising relative sea levels. A better understanding of organic-matter dynamics in salt marshes is key to address salt-marsh conservation issues and to elucidate marsh importance within the global carbon cycle. Toward this goal, we empirically derived rates of organic matter decomposition by burying 712 commercially available tea bags at different marshes in the microtidal Venice Lagoon (Italy), and by analyzing them following the Tea Bag Index protocol. We find values of the decomposition rate (k) and stabilization factor (S) equal to 0.012 ± 0.003 day^{-1} and 0.15 ± 0.063, respectively. Water temperature critically affects organic matter decomposition, enhancing decomposition rates by 8% per °C on average. We argue that, at least in the short term, the amount of undecomposed organic matter that actively contributes to carbon sequestration and marsh vertical accretion strongly depends on the initial organic matter quality, which is a function of marsh and vegetation characteristics.

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Analysis of Organic Matter Decomposition in the Salt Marshes of the Venice Lagoon (Italy) Using Standard Litter Bags

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Key Points:

- Decomposition rates in Venice marshes display a mean value of 0.012 ± 0.003 day^{-1}, confirming them among biomes with the slowest decomposition rates.

- We find that a one degree increase in temperature leads to a 8% increase in decomposition rates.

- Litter quality exerts a primary control on the amount of preserved organic matter contributing to carbon sequestration and marsh accretion.

Abstract

Tidal salt marshes are widespread along the World's coasts, and are ecologically and economically important as they provide several valuable ecosystem services. In particular, their significant primary production, coupled with sustained vertical accretion rates, enables marshes to sequester and store large amounts of organic carbon and makes them one of the most carbon-rich ecosystems on Earth. Organic carbon accumulation results from the balance between inputs, i.e. organic matter produced by local plants or imported, and outputs through decomposition and erosion. Additionally, organic matter deposition actively contributes to marsh vertical accretion, thus critically affecting the resilience of marsh ecosystems to rising relative sea levels. A better understanding of organic-matter dynamics in salt marshes is key to address salt-marsh conservation issues and to elucidate marsh importance within the global carbon cycle. Toward this goal, we empirically derived rates of organic matter decomposition by burying 712 commercially available tea bags at different marshes in the microtidal Venice Lagoon (Italy), and by analyzing them following the Tea Bag Index protocol. We find values of the decomposition rate (k) and stabilization factor (S) equal to 0.012 ± 0.003 day^{-1} and 0.15 ± 0.063, respectively. Water temperature critically affects organic matter decomposition, enhancing decomposition rates by 8% per °C on average. We argue that, at least in the short term, the amount of undecomposed organic matter that actively contributes to carbon sequestration and marsh vertical accretion strongly depends on the initial organic matter quality, which is a function of marsh and vegetation characteristics.

Plain Language Summary

Salt marshes are important coastal environments regularly flooded by the tide and dominated by herbaceous plants, providing several valuable ecosystem services. They are, however, threatened by the effects of climate changes and human interferences. As organic matter accumulated in salt-marsh soil importantly contribute to surface elevation necessary for marshes to keep up with sea level rise and to store atmospheric carbon, this project aims to improve our understanding of decomposition processes affecting organic matter preservation and their controls in salt-marsh environment. Toward this goal, following the so-called Tea Bag Index protocol, we buried 712 commercially available tea bags in salt-marsh soils of the Venice Lagoon (Italy) measuring the reduction of their organic content due to decomposition processes after three months. Our results confirm that salt marshes are among biomes with the slowest decomposition rates. However, we observed a loss of about two-thirds of the initial labile organic mass after 90 days and that initial litter quality, depending on litter and vegetation characteristics, exerts a primary control on the amount of preserved organic matter contributing to carbon sequestration and marsh accretion.

1 Introduction

Salt marshes are transitional ecosystems found between permanently submerged and emerged coastal environments. They are the prevailing landscape in the intertidal zone of many low-energy temperate coasts (Adam, 1990; Allen & Pye, 1992; Mcowen et al., 2017), with vegetation dominated mostly by herbaceous halophytes adapted to regular inundation by saltwater (Perillo et al., 2009). Salt marshes are crucial ecomorphodynamic structures in tidal environments as they offer valuable ecosystem services (Barbier et al., 2011) by attenuating waves (Möller et al., 2014; Temmerman et al., 2013), acting as sediment trapping zones (Allen, 2000; Mudd et al., 2009), boosting the production of economically and ecologically important fishery species (Boesch & Turner, 1984; MacKenzie & Dionne, 2008), and filtering both nutrients and pollutants (Costanza et al., 1997). In addition, marshes serve as highly efficient sinks for blue carbon, i.e., the organic Carbon (C) captured and stored by coastal ecosystems and oceans (Chmura et al., 2003; Duarte et al., 2005; Macreadie et al., 2019; McLeod et al., 2011). Such a potential for carbon sequestration derives from the high rates characterizing marsh primary production, coupled with sustained vertical accretion rates driven by the deposition of both Organic Matter (OM) and clastic sediments (e.g., D'Alpaos et al., 2007; Kirwan & Murray, 2007; Marani et al., 2007; Morris et al., 2002; Mudd et al., 2009), as well as from the fact that carbon storage occurs predominantly in belowground biomass and that soil is typically in anaerobic conditions (McLeod et al., 2011; Roner et al., 2016; Rogers et al., 2019; Wang et al., 2019; Ouyang & Lee, 2020). This allows marshes to sustain some of the highest rates of carbon sequestration per unit area of all ecosystems, making them an important player in the global carbon cycle and in strategies aimed at reducing CO_2 emissions (Macreadie et al., 2019; McLeod et al., 2011). Despite their importance, coastal ecosystems are some of the most heavily used and threatened natural systems globally, experiencing widespread loss or degradation (Barbier et al., 2011; Duarte et al., 2005; Valiela et al., 2001). Marsh ecosystems are seriously exposed to the effects of climate changes and human interferences, sea level rise and lack of available sediments being the key factors in determining salt-marsh drowning and disappearance (D'Alpaos et al., 2011; Kirwan et al., 2010; Marani et al., 2007; Morris et al., 2002; Mudd, 2011; Tognin et al., 2021, 2022). Therefore, understanding of the processes regulating OM accumulation and C sequestration in salt marshes is critical to better estimate their resilience to climate change, as well as their contribution to the global carbon cycle, providing valuable information to improve management and conservation strategies (Cahoon & Guntenspergen, 2010; Couvillion et al., 2013; C. D'Alpaos & D'Alpaos, 2021; McLeod et al., 2011; Morris et al., 2016; Mueller et al., 2019; Nyman et al., 2006; Pendleton et al., 2012; Turner et al., 2002). However, the exact dimensions of the salt-marsh role on the global carbon cycle and of their contribution to offset CO_2 emissions, are still uncertain, also because of our current limited knowledge on the decomposition of organic matter in marsh soil and on how decomposition rates can be affected by climate changes and human disturbances (Djukic et al., 2018;

Macreadie et al., 2019; Sifleet et al., 2011). This work deals with this important issue.

More in detail, salt-marsh blue carbon is sequestered over the short term in living biomass aboveground (leaves, stems, branches) and belowground (roots) and over longer time scales within soil organic matter (SOM) in sediments (McLeod et al., 2011). Local plant biomass and the OM imported by tidal currents and waves (Tognin et al., 2021) are the main sources of the SOM in marshes (Morris et al., 2016; Yousefi Lalimi et al., 2018). Organic inputs, together with inorganic sediments deposited over the marsh platform by tidal flooding and waves and captured by vegetation, are the main processes contributing to marsh accretion and forming marsh soil where carbon is stored (e.g., Kirwan et al., 2013; Mudd et al., 2009; Roner et al., 2016).

Accumulation of SOM is strongly influenced by decomposition processes, which determine the fraction of the OM produced or imported that effectively contributes to soil formation and carbon burial (Kirwan et al., 2013; Mudd et al., 2009; Rybczyk & Cahoon, 2002).

Decomposition of organic matter is the process of physical breakdown and biochemical transformation of complex organic molecules which compose dead OM (litter) into simpler organic and inorganic molecules. Specifically, decomposition consists of three concurrent processes, namely, communition (or fragmentation), leaching of water-soluble compounds, and microbial catabolism (Sanderman & Amundson, 2013). Decomposition results in the release of CO_2 and other organic gases (e.g. methane, nitrogen, sulfides), water, mineral nutrients, and energy, playing a fundamental role in biogeochemical cycles (Pavao-Zuckerman, 2008). Decomposition is controlled by the interactions between the physical environment, the quality of the substrate, and the community of decomposer organisms, and it is therefore characterized by widely varying rates and extents. Organic matter is composed of a complex mixture of biopolymers. Some of these compounds, such as proteins, carbohydrates, and lipids are easily degraded by microorganisms (i.e., labile), while other compounds, such as lignin and hemicellulose, are resistant to decomposition (i.e., recalcitrant) (Megonigal et al., 2004). Given enough time and the proper environmental conditions, most naturally occurring labile compounds can be completely mineralized to inorganic forms, except for a fraction of the organic residues, which is transformed into stable SOM (i.e., stabilization; Sanderman & Amundson, 2013). Studies on litter decay have often emphasized the importance of climate on decomposition processes (Sanderman & Amundson, 2013), and temperature has long been thought to be an important control of decay rates in wetlands (Montagna & Ruber, 1980; White et al., 1978). Recent experimental results on a global scale suggest that the decomposition rate and the stabilisation factor are sensitive to temperature, the first increasing and the second decreasing with warming (Keuskamp et al. 2013; Mueller et al. 2018). The results of a short cellulose decay experiment, conducted along the East Coast of the United States, showed a significant relationship between mean daily temperature and decay rate equivalent to a 19% increase in mass loss for each degree warming (Kirwan et

al., 2014). Nevertheless, large variations in litter mass loss were observed within biomes, across marshes and across different sites (e.g, Kirwan et al., 2014; Morris et al., 2002; Mueller et al., 2018; Reents et al., 2021), suggesting that local-scale factors other than climate have strong controls on decomposition dynamics (Cornwell et al., 2008; Djukic et al., 2018). Soil characteristics, in terms e.g. of aeration and drainage, and flooding conditions (hydroperiod), which are influenced by local topography and tidal levels, affect both biomass production and decomposition rates (Kirwan et al., 2013; Marani et al., 2006a; Mudd et al., 2009; Yousefi Lalimi et al., 2018). Several studies suggest that the relationship between the decomposition rate and elevation can be highly variable (Yousefi Lalimi et al., 2018). Halupa and Howes (1995), for instance, found that the rates of carbon loss measured in a New Jersey salt marsh through litterbag experiments and laboratory incubation were related to flooding frequency and duration. However, Kirwan et al. (2013) found an uncertain and weak relationship between decomposition rates and flooding duration in the Chesapeake Bay brackish tidal marshes. Mueller et al. (2018), who examined the results of standardized litterbag experiments on 30 tidal-wetland sites worldwide, found no relation between decomposition rates and elevation, but showed that the stabilisation factor was reduced in low-elevation and more frequently flooded zones compared to high-elevation zones. Yousefi Lalimi et al. (2018) found no clear trends of decomposition rates and stabilisation factors related to elevation and flooding along three transects on coastal marshes located in North Carolina (USA). Furthermore, the characteristics of the organic matter itself are also known to strongly influence decomposition processes, and some authors indicate chemical and structural composition of the plant material as the main driver for decomposition rates (Freschet et al., 2012; Lang et al., 2009; Wang et al., 2017). These uncertainties in unravelling the governing processes for OM decomposition call for further analyses.

Here we aim at providing new insights on OM fate in salt-marsh soils, clarifying which are the physical and biological factors that control OM decomposition, and how decomposition affects the amount of OM effectively contributing to soil formation and carbon burial in tidal marshes.

Toward these goals, we utilized the Tea Bags Index (TBI) approach (Keuskamp et al., 2013) to estimate the rates of OM decomposition and stabilization in salt-marsh soils within the microtidal Venice Lagoon (Italy), relating them to different environmental conditions measured directly in the field. By contributing to a better understanding of OM fate in tidal marshes, our results will be useful to inform models describing marsh ecosystem functioning and evolution (e.g. D'Alpaos & Marani, 2016; Fagherazzi et al., 2012; Marani et al., 2010; Mudd et al., 2009). An improved representation of soil organic matter dynamics in biomorphodynamic models may be fundamental in evaluating marsh resilience in the face of climate changes and anthropogenic disturbances. In addition, the description of soil organic matter decomposition is a key element for assessing carbon sequestration potential of salt-marshes.

2 Materials and Methods

2.1 Study site

The litterbag experiments were conducted in the Venice Lagoon (Figure 1), in the north-western Adriatic Sea (Italy). With an area of about 550 km^2 and an average water depth of 1.5 m, the Venice Lagoon is the largest lagoon in the Mediterranean and is characterised by a semidiurnal tidal regime with a mean tidal range of about 1.0 m. The lagoon is connected to the sea by three inlets: Lido, Malamocco, and Chioggia.

Tea bags were deployed at 7 different marsh sites within the lagoon (Figure 1). Most of the studied marshes - namely S. Felice, Saline, Scanello, S. Erasmo, Lazzaretto Nuovo, Pagliaga and Campalto (see Figure 1) are located in the northern and most naturally-preserved part of the lagoon, and are found at variable distances from the Lido inlet, whereas the Fossei salt marsh is located in the southern lagoon (Figure 1).
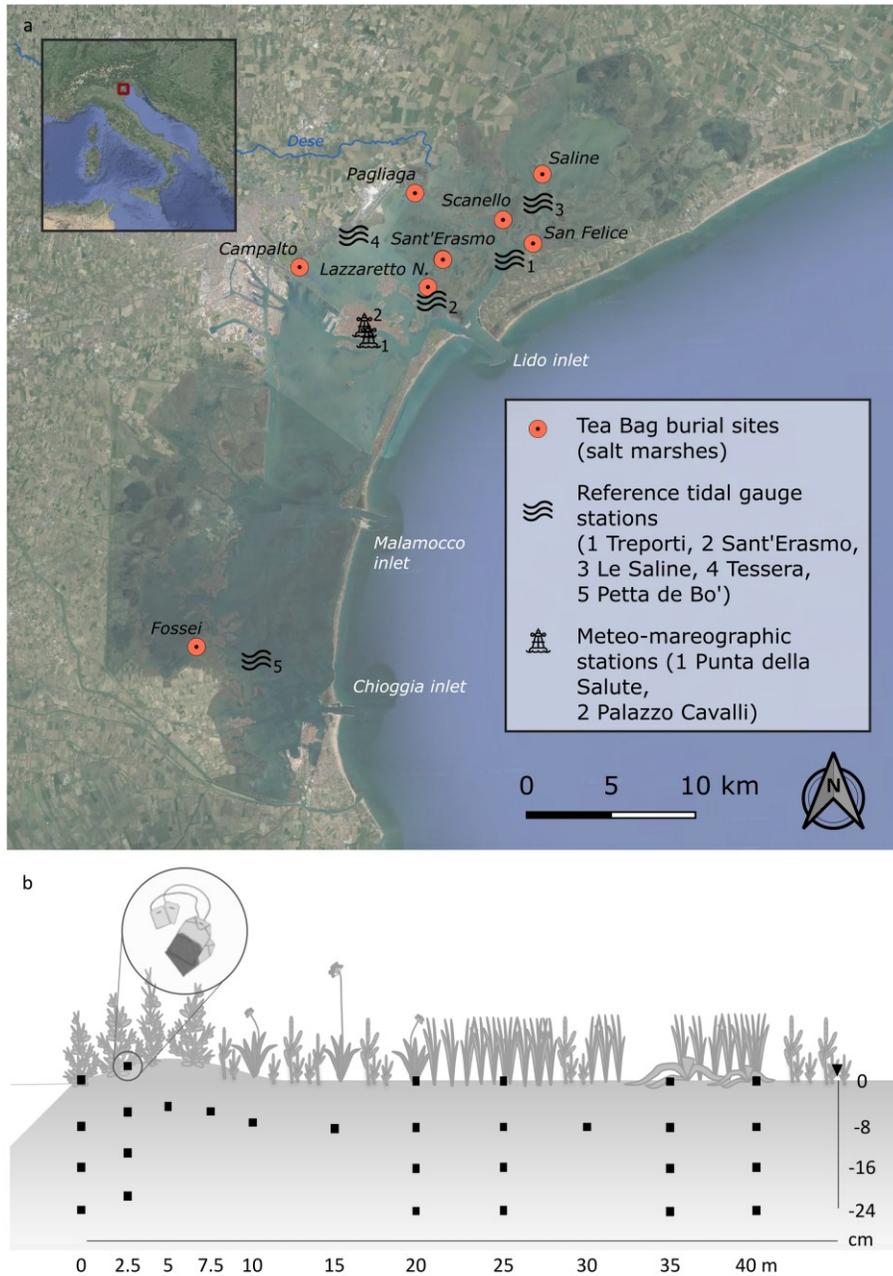
Figure 1. **Study area and configuration of the burial experiment**. Location of the study sites in the Venice lagoon, Italy (a), and a sketch of the scheme used for the burial experiments conducted along one of the analyzed marsh transects (b). Point 0 of each transect is sited at the edge of the marsh.

The salt marshes in S. Felice, Saline, Scanello, S. Erasmo, and Lazzaretto Nuovo are adjacent to large tidal channels departing from the Lido inlet, and their origin has been ascribed to marine sediment inputs transported by flood tides (Bonometto, 2005; Silvestri et al., 2005). These marshes show typically concave-up profiles, with raised edges and lower elevations toward the inner portion of the marsh (Bonometto, 2005), and host exclusively halophytic vegetation, mainly constituted by *Salicornia veneta, Limonium narbonense,* and *Sarcocornia fruticosa,* associated with *Spartina maritima, Juncus maritimus, Puccinellia palustris, Inula crithmoides, Suaeda maritima* and *Arthrocnemum macrostachyum* (Silvestri, 2000; Silvestri et al., 2005). In contrast, the Pagliaga salt marsh is located at the landward boundary of the lagoon, close to the estuary of the springwater Dese River which debouches into the Lagoon carrying an average freshwater discharge of about 6.5 m^3/s and negligible sediment supply (Figure 1). Freshwater inputs maintain a near-freshwater plant community dominated by *Phragmithes australis*, together with the halophytic species *Juncus maritimum, Salicornia veneta,* and *Halimione portulacoides* (Silvestri, 2000). Similarly, the Campalto salt marsh is found along the lagoon-mainland boundary, though it was originated on continental grounds of the coastal plains that were reached and permeated by brackish waters (Bonometto, 2005). The Campalto marsh hosts halophytic species dominated by *Limonium narbonense,* associated with *Sarcocornia fruticosa, Spartina maritima, Salicornia veneta,* and scarce *Suaeda maritima.* Finally, the Fossei East and Fossei West salt marshes are located in the southern part of the Venice Lagoon, about 7 km NW of the Chioggia inlet, within a wetland area originated from pre-existing brackish environments or salinized freshwaters arising from river diversions (Bonometto, 2005; Roner et al., 2021). These marshes were artificially established between 1994 and 1996 to limit the lateral erosion of wind-exposed natural marshes, and they have been colonized by the typical halophytic vegetation species mainly constituted by *Salicornia veneta, Limonium narbonense, Sarcocornia fruticosa, Suaeda maritima and Puccinellia palustris* (Cecconi et al., 1998).

2.2 Tea Bag Index

To estimate decomposition rates and organic matter stabilisation in salt marsh soils, the Tea Bag Index (TBI) protocol proposed by Keuskamp et al. (2013) was adopted. The protocol consists of a simplified litter-bag experiment carried out utilizing standard litter in the form of commercially available tea bags (Lipton, Unilever). Two types of tea material with distinct qualities were used: green tea, with high cellulose content that is expected to undergo fast decomposition, and rooibos tea, characterized by high lignin content and expected to decompose slowly. Each tetrahedron-shaped synthetic tea bag contains about 2 g of tea and has a mesh size of 0.25 mm, allowing microorganisms and mesofauna to enter

the bag and decompose the organic matter contained therein (Keuskamp et al., 2013).

Green and rooibos tea bags were buried pairwise in salt-marsh soils along linear transects and retrieved after about 90 days, with four transects having an incubation period <80 days (San Felice 1 and 2, Sant'Erasmo1 and 2 Jun 17 - Sept 2 2015) and one transect >100 days (San Felice - Tavolini Jun 24 - Oct 11 2016), see Table 1. We buried 712 tea bags in total (356 green tea; 356 rooibos tea) along transects oriented perpendicularly to the marsh margin (Table 1). According to Keuskamp et al. (2013), the standard burial depth corresponds to 8 cm below the marsh surface. However, at some sites, tea bags were also placed at different depths, corresponding to 0, 16, 24, and 40 cm relative to the marsh surface (Table 1) to analyse the effects of burial depths on decomposition dynamics. The tea bags were deployed between April and October in 2015, 2016, and 2017. In some cases, experiments were repeated in different periods along the same transect (Table 1).

The initial weight of the tea bag content was determined by subtracting the mean weight of 10 empty bags (bag + string + label) from the weight of the intact tea bag prior to deployment (tea + bag + string + label). Once retrieved, the content of tea bags was extracted, oven-dried for 48 h at 70° C, and weighted. To eliminate the effects of small amounts of inorganic sediments that could have entered the bags during the experiments, a Loss On Ignition procedure (LOI, by heating samples in a muffle oven at 550°C for 3 h) was conducted on the contents of the retrieved bags after drying and recording the weights. The material remaining after combustion includes inorganic sediments that entered the bags after burial, as well as tea material that is not easily burned. We estimated this latter term by measuring the remaining material after the application of a LOI procedure to a group of 10 intact tea bags prior to deployment. We subtracted the weights of uncombusted material from the weights of the material remaining after combustion of the retrieved bags, to estimate the weight of inorganic sediment/salt that had entered each bag after burial. We finally used the weight of the extraneous mass to correct the weight of the tea bag organic content after incubation.

The results were finally used to estimate the Tea Bag Index according to the methodology proposed by Keuskamp et al. (2013).

The Tea Bag Index consists of two parameters describing the decomposition rate (k) and the litter stabilisation factor (S). By using two distinct tea types with contrasting decomposability, it is possible to estimate k and S using a single measurement in time. Specifically, the fractional weight, *W(t)*, of a buried bag

content is assumed to change through time as a result of decomposition processes according to an exponential decay function with constant decomposition rate k:

$$W(t) = ae^{-kt} + (1 - a) \qquad (1)$$

Where t denotes time, and a and $(1 - a)$ are the labile and the recalcitrant fraction of the substrate, respectively. This approach assumes that decomposition of non-hydrolysable materials is negligible for burial periods shorter than 3 months.

During decomposition, parts of the labile compounds stabilise and become recalcitrant (Prescott, 2010), resulting in a deviation of the actual decomposed fraction a (i.e., limit value) from the hydrolysable fraction H (i.e., chemically labile). This deviation represents the stabilisation factor S, which, following Keuskamp et al. (2013) can be computed as:

$$S = 1 - \frac{a}{H} \qquad (2)$$

The calculation of both the decomposition rate (k) and the stabilisation factor (S) is carried out following Keuskamp et al. (2013), who found that, after 3 months, the labile fraction of green tea, a_g, is almost completely decomposed. Hence, the labile fraction of green tea can be determined at the end of the incubation experiment. Using equation (2), and considering the green tea hydrolysable fraction H_g obtained from chemical analysis, the stabilisation factor S_g for green tea can be determined. The value of S is then assumed to be equal for both types of material used, being dependent only on environmental conditions (i.e., $S_g = S_r$). Consequently, the labile fraction a_r of rooibos tea can be estimated using eq. (2) and decomposition constant rates k can be estimated using eq. (1).

| | 2015 | | | 2016 | | | | 2017 | | |
	Apr 29 - Jul 29 23,75°C	Jun 11 - Sept 9 26,35°C	Jun 17 - Sept 2 26,55°C	Jun 24 - Sept 23 25,91°C	Jun 24 - Oct 11 25,07°C	Jun 30 - Sept 28 25,69°C	Jul 13 - Oct 11 24,76°C	Apr 12 - Jul 10 21,43°C	Apr 12 - Jul 19 21,91°C	Jul 10 - Oct 12 24,34°C
S. Felice - Spaccotralo	-8 cm									
S. Felice - Spaccotralo 1			-8 cm					-8, -16 cm		0, -8, -16, -24 cm
S. Felice - Spaccotralo 2			-8 cm	-8 cm				-8, -16 cm		0, -8, -16, -24 cm
S. Felice - Tavolini	-8 cm				-8 cm					
Saline				-8 cm				-8, -16 cm		0, -8, -16, -40 cm
Sant'Erasmo 1		-8 cm								
Sant'Erasmo 2		-8 cm								
Scanello	-8 cm									
Pagliaga	-8 cm									
Campalto								-8, -16 cm		
Lazzaretto Nuovo							-8 cm			
Fossei E						-8 cm				
Fossei W						-8 cm				

Table 1. **Burial experiment design**. Incubation sites (Figure 1) with relative incubation periods, mean water temperature during the incubation period, and burial depth.

2.3 Environmental parameters

In order to separate the role of different environmental conditions on the decomposition rate and stabilisation factor, a number of environmental parameters were determined.

Mean water temperature was determined for each incubation period by calculating the mean value of the water temperature measured every 10 minutes at Punta della Salute station by the CPSM - Centro Previsioni e Segnalazioni Maree of the Venice Municipality.

Elevation above Mean Sea Level (MSL) of each burial site was determined using two TOPCON GR-3 GPS receivers (dual frequency - L1/L2 - and dual constellation - NavStar/Glonass - with integrated Tx/Rx UHF radio). The real tea bag burial elevation (z_β) was then calculated by subtracting the burial depth (ranging from 0 to 40 cm) to the elevation of the marsh surface.

The distance of each burial site from the edge of the nearest channel (ζ) was determined during field surveys. In order to collect information on flooding frequency and duration, based on the elevation of the burial sites, we calculated the percentage of the burial period during which each site was flooded by water (φ) (except for Fossei, Lazzaretto Nuovo and Campalto transects, where elevation data were not available), comparing local marsh elevations with tidal levels measured at 10-minute frequency by the nearest tidal gauge station of the CPSM - Centro Previsioni e Segnalazioni Maree monitoring network (Figure 1).

2.4 Statistical analyses

To test for the effects of environmental parameters on k and S, the Kendall correlation coefficient (τ) (Kendall, 1938) was determined. The Kendall test is a non-parametric, rank-based method, aimed at determining whether there exists a monotonic relationship between two variables of interest. The value of the τ coefficient ranges from 1 to −1, indicating a positive or a negative association, respectively. Because of the large number of ties in our study, a modified equation that considers the number of ties was used (Soliani, 2019; Sprent & Smeeton, 2000).

In addition, we also employed the Wilcoxon signed-rank test to analyse the difference between decomposition metrics measured at different depths. The Wilcoxon signed-rank test is a non-parametric statistical hypothesis test used to compare two populations when the observations are paired, and it is appropriate

for a repeated measure design where the same variables are evaluated under two different conditions.

4 Results and discussion

4.1 Tea Bag Index metrics for the Venice Lagoon

We first computed the decomposition metrics, namely the decomposition rate (k) and the stabilisation factor (S), for all the tea bag pair samples retrieved in the Venice lagoon (Figure 2 a,c), together with their frequency distributions (Figure 2 b,d). Decomposition rates vary between 0.003 and 0.027 days^{-1}, with a median value of 0.012±0.003 days^{-1}, whereas the stabilisation factors range between 0.016 and 0.544, their median value being equal to 0.15±0.063.

A comparison between the values of k and S obtained for the Venice lagoon with those reported by Keuskamp et al. (2013) for different ecosystems is reported in Figure 3, together with data derived for different salt-marsh ecosystems by Mueller et al. (2018) and Yousefi Lalimi et al. (2018). Our results confirm that salt marshes exhibit some of the lowest decomposition rates among different biomes, although they are also characterized by reduced stabilisation factors (Keuskamp et al., 2013; Mueller et al., 2018; Yousefi Lalimi et al., 2018). Indeed, Mueller et al. (2018) and Yousefi Lalimi et al. (2018) obtained average k values of 0.012 ± 0.007 and 0.011 ± 0.002 for their salt-marsh sites, respectively, which nicely meet our findings. These decomposition rates are smaller than those obtained for temperate, mixed and tropical forests and for mangroves (Figure 3) (Keuskamp et al., 2013). As far as stabilization factors are concerned, our average value is slightly larger than Yousefi Lalimi et al. (2018)'s one and close to Mueller et al. (2018)'s one.

Assuming the labile OM fraction to decompose according to an exponential-decay model $W(t) = e^{-kt}$ (where W is the remaining fraction of the organic mass at time t and k is the decomposition rate), the computed value of k= 0.012 days^{-1} for the Venice lagoon implies that 66% of the initial organic mass would decompose after 90 days. Conversely, a mean stabilisation factor of S=0.15 leads, during an incubation timespan of 90 days, to the stabilization of about 15% of the labile material, the latter being therefore not affected by decomposition processes on the short term.

Following the above-recalled asymptotic model proposed by Keuskamp et al. (2013) described by Eq. (1), our results suggest that, in the short term, the remaining mass of organic matter strongly depends on the initial recalcitrant fraction $(1 - a)$. Indeed, after the complete decomposition of the labile fraction,

the remaining mass is equal to the recalcitrant fraction summed to the stabilised labile fraction.
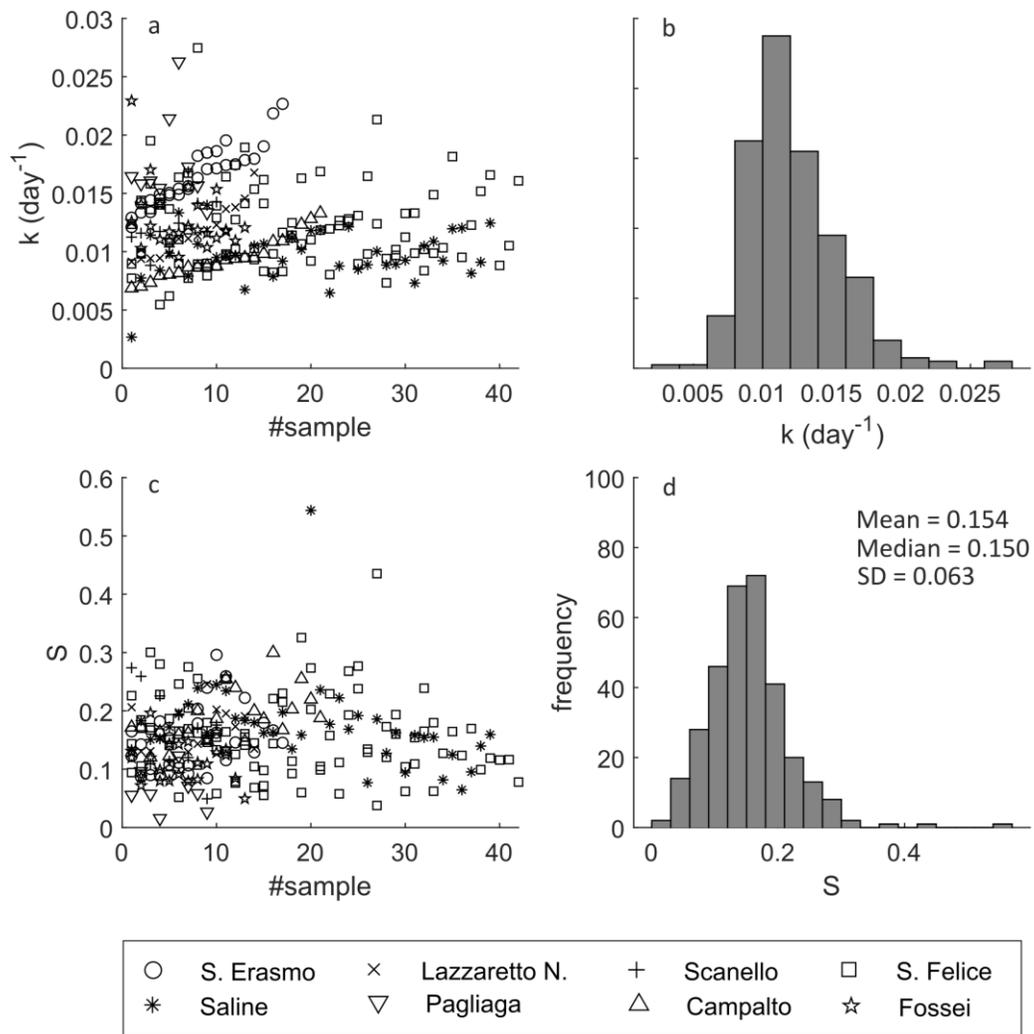
Figure 2. **The Tea Bag Index metrics for the analysed samples in the Venice Lagoon**. a) Decomposition rates (k) for all the samples; b) Frequency distribution of the decomposition rates (k); c) Stabilisation factors (S) for all the samples; d) Frequency distribution of the stabilisation factors (S).
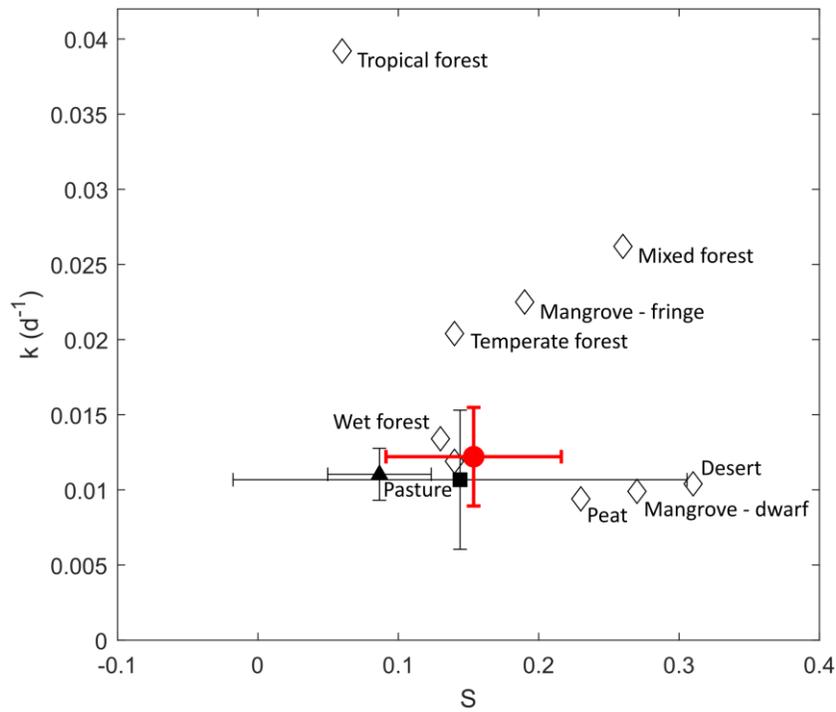
Figure 3. **Decomposition metrics in major biomes**. The mean values of the decomposition rate (k) and of the stabilisation factor (S) found in this study (red dot), compared with data from different ecosystems according to Keuskamp et al. (2013, empty diamonds) and for different marshes around the world, based on data from Yousefi Lalimi et al. (2018, solid triangle, from three transects in North Carolina (USA) marshes) and Mueller et al. (2018, solid square, data from 30 tidal-wetland sites worldwide, most of which were salt marshes). Error bars indicate standard deviations.
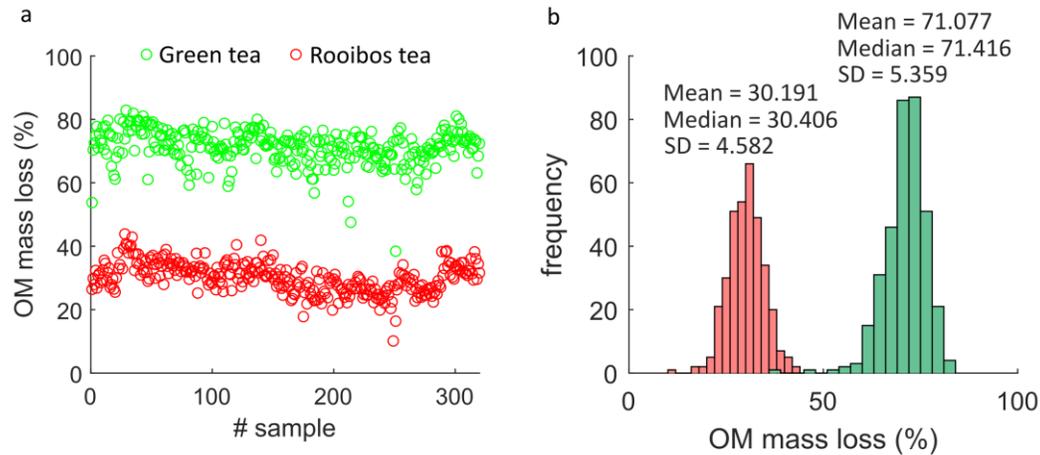
Figure 4. **Organic matter mass loss results**. Percent tea mass loss after 90 days of field incubation for the analysed samples of green tea (green empty circles) and rooibos tea (red empty circles) are reported in panel a, with the related frequency distributions shown in panel b.

As expected, mass loss after three months of field incubation (Figure 4) was higher for green tea (71.08±5.36%) than for rooibos tea (30.19±4.58%).

Our results are overall consistent with findings by Kirwan et al. (2014) and Kirwan and Blum (2011), who measured the organic mass loss in litter bag decomposition experiments in the North American Atlantic coasts by computing the decay coefficient as $k^* = [-ln(C_t/C_o)]/t$ where C_t and C_o are the mass of organic matter at the end and at the beginning of the experiment, respectively. Their approach, however, did not account for the proportion of recalcitrant and labile material. Calculating the decay coefficient k^* for our tea bag experiments, we obtained different values for the green tea (0.014 ± 0.002 days^{-1}) and the rooibos tea (0.004 ± 0.001 days^{-1}). As expected, this confirms that green tea is more labile, whereas rooibos is more recalcitrant (Figure 4). Moreover, values from our samples nicely match the decay coefficients k^* found by Kirwan and Blum (2011) for *Spartina alterniflora* stem and leaf material (0.004 ÷ 0.016 days^{-1}) and by Kirwan et al. (2014) for *Schoenoplectus americanus* root and rhizome material (0.003 ÷ 0.007 days^{-1}). In the case of salt-marsh vegetation, aboveground litter was observed to generally decompose faster than belowground litter (Scarton et al., 2002; Stagg et al., 2018). Therefore, green and rooibos tea showed consistent decay coefficients with respect to aboveground and belowground salt-marsh plant litter, respectively. Although the aim of Tea Bag Index analysis is to elucidate climate and environmental effects on decomposition processes, by use of a standard organic material (thereby removing any influence by litter quality), this comparison further confirms that tea material can be considered representative of organic matter in salt-marsh

environments and further highlights the influence of litter quality on organic matter conservation.

4.2 Relationships between environmental parameters and decomposition processes

We analysed the effects of environmental variables such as temperature, elevation, distance from the marsh edge, and flooding period on both the decomposition coefficient (k) and on the stabilisation factor (S) (Figure 5 and Figure 6). By fitting linear regression models to our field data, we show that the average water temperature during the incubation period (T) holds the most statistically significant relation with both k and S. Specifically, we found that the decomposition rate, k, increases with T, whereas the stabilisation factor, S, decreases as temperature increases (Kendall's tau test, p-value < 0.01). Notably, these relationships hold in spite of the relatively narrow range of temperature variability observed in our dataset, with $21<T<27$ °C for all the experiments carried out in this study. Such significant control of T on both S and k is consistent with previous findings highlighting the critical role of temperature on OM decay rates in tidal wetlands (Keuskamp et al., 2013; Kirwan et al., 2014; Kirwan & Blum, 2011; Montagna & Ruber, 1980; Mueller et al., 2018; White et al., 1978). Being a chemical process mediated by microbial enzymes, the decomposition of SOM is known to be strongly affected by temperature (e.g., Davidson & Janssens 2006; Moinet et al. 2020). Indeed, temperature can affect litter decomposition both directly, by regulating the activity of decomposers, and indirectly, through changes in other temperature-sensitive conditions influencing decomposition processes, such as soil moisture and oxygen diffusion. Oxygen diffusion from the atmosphere, plant aerenchyma, or aerated water, which increases with increasing temperature, affects oxygen availability for decomposition reactions. In saturated or partially saturated soils, oxygen availability represents a rate-limiting factor for decomposition processes (Kirwan et al., 2014). Indeed, flooding slows oxygen diffusion by suppressing microbial respiration and allowing only anaerobic decomposition, which includes fewer and generally slower degradative enzymatic pathways (Davidson & Janssens, 2006; Morris et al., 2016). Differences in flooding frequency along elevational gradients in tidal wetlands have proved to induce sharp gradients in oxygen availability and redox conditions (Kirwan & Megonigal, 2013; Morris et al., 2016). Therefore, the intrinsic spatial variability in salt-marsh topography is likely to influence microclimatic conditions affecting decomposition processes.

$\tau = -0.4835$; p-value = **2*10^{-24}** *(n = 223)* $\qquad$ $\tau = -0.2313$; p-value = **1*10^{-6}** *(n = 223)*
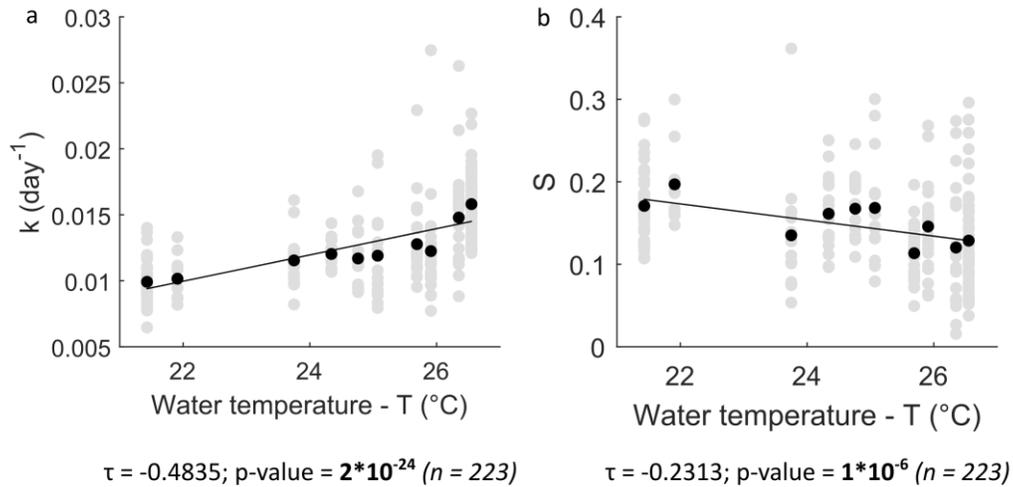
Figure 5. **Effect of temperature on decomposition metrics**. Decomposition rate (k) (a) and stabilisation factor (S) (b) as a function of the mean water temperature (T) measured during the incubation period. Black closed circles represent averages for a given temperature value. In the lower inset, results of Kendall's tau test are also reported. **Bold text indicates p-values** lower than the chosen significance level ($p < 0.01$). The number of samples (n = 223) is also reported.

Indeed, we found a statistically-significant relationship between the decomposition rate (k) and both the burial elevation (z_β) (Figure 6a; Kendall's tau test, p-value = 0.0025; k increasing with elevation) and the distance from the closest marsh edge (ζ) (Figure 6c; Kendall's tau test, p-value = 0.0010; k decreasing with increasing distance), the latter being a proxy for the distance to the nearest source of water and mineral sediments. Conversely, no significant relation was found between the stabilisation factor (S) and either burial elevation (z_β) or the distance from the marsh edge (ζ) (Figure 6b, d). The stabilisation factor S is also negatively correlated to the duration of marsh flooding (φ) (Figure f), whereas flooding (φ) displays no significant correlation with the decomposition rate k (Figure 6e).
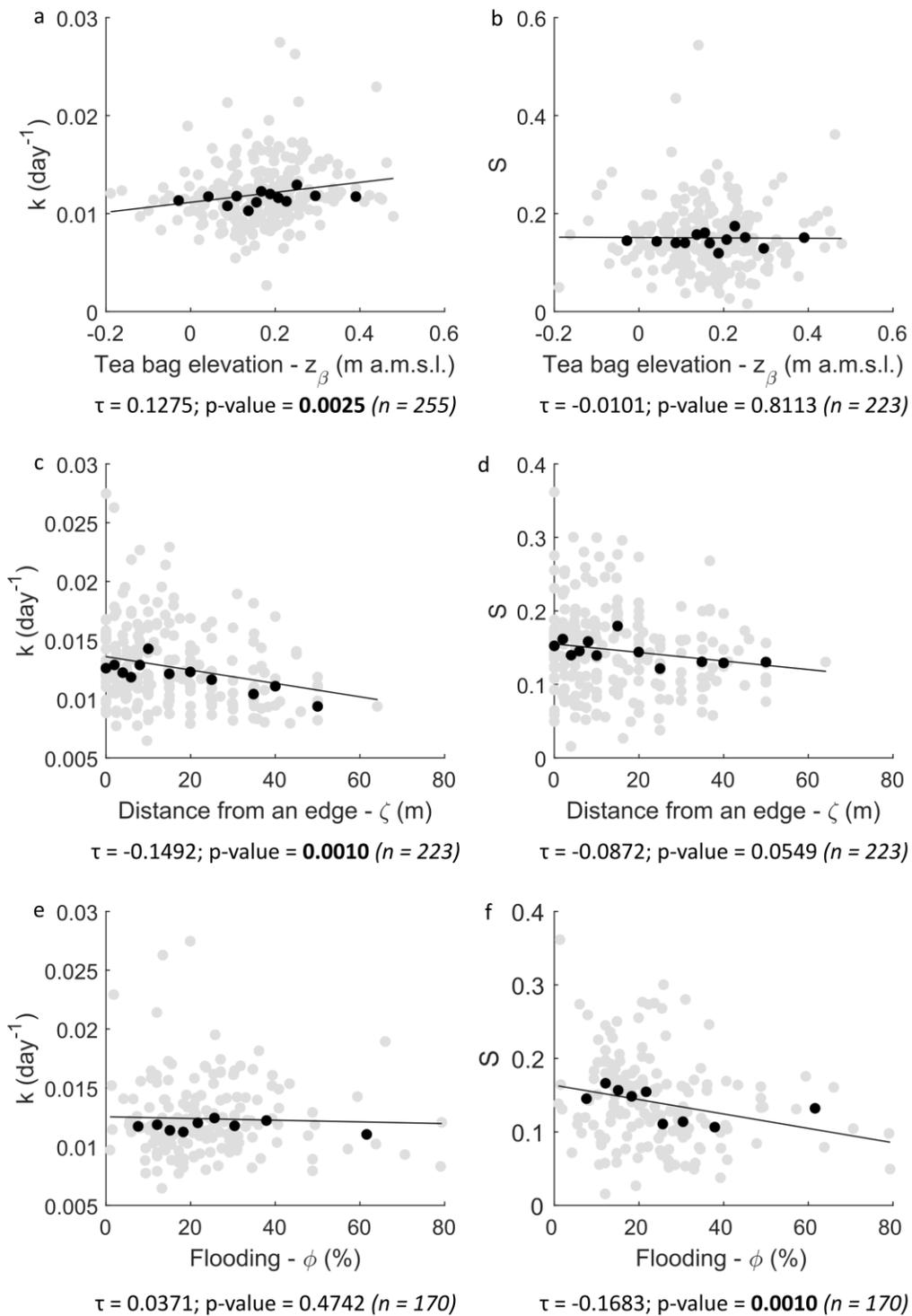
Figure 6. **Effects of environmental conditions on organic matter decomposition**. Decomposition rate (k) and stabilisation factor (S) as a function of a,b) burial elevation (z_β) (all samples n=255 considered); c,d) distance from

the edge (ζ) (only samples buried at 8 cm depth considered, $n=223$); e,f) salt-marsh flooding (φ), computed as the percentage of the burial period during which each site was submerged by water, (only samples buried at 8 cm depth considered, $n=170$). Black closed circles represent binned averaged values obtained by averaging sets of 20 values. In each panel, the results of the Kendall's tau test are reported in the lower inset, with **bold text indicating *p*-values** lower than the chosen significance level (p < 0.01).

The dependence of k on both z_β and ζ is somehow expected in view of the typical concave-up morphology characterizing most of marsh ecosystems, where surface elevation decreases progressively moving away from the marsh edge towards the inner marsh. Clearly, marsh elevation also exerts a primary control on flooding frequency and duration (Chmura & Hung, 2004; D'Alpaos et al., 2007; Marani et al., 2006a). Thus, these interdependencies may suggest that larger oxygen availability in more elevated, which are less frequently flooded sites, promotes the decomposition of organic matter, enhancing microbial respiration. Other factors linked to these morphological features that could potentially influence decomposition processes are vegetation characteristics (i.e., above and belowground production, C-N ratio) and nutrient availability, which may affect microbial community (Kirwan et al., 2014; Mueller et al., 2018; Yarwood, 2018). However, the control of marsh flooding on OM decomposition is not as clear as in the case of elevation and distance from the edge, with φ not being significantly correlated to k. Nevertheless, we should highlight that φ was derived indirectly by comparing site-specific measurements of marsh elevation with tide level data retrieved from nearby tidal gauge stations. Therefore, a degree of uncertainty is to be expected for φ, which might not be an optimal representation of the actual time during which the marsh soil is submerged, the latter process depending also on local marsh microtopography and on the characteristics of the extensive networks of tidal creeks that typically cut through the marsh platform.

Moreover, it is worthwhile noting that soil aeration is affected also by plant evapotranspiration and water table dynamics. Groundwater flow and evapotranspiration are known to promote the formation of an aerated layer below the soil surface, thus allowing for a prolonged presence of oxygen for aerobic respiration even when the marsh is flooded (Boaga et al., 2014; Marani et al., 2006b; Ursino et al., 2004). Ursino et al. (2004) and Marani et al. (2006b) showed that in the absence of evapotranspiration, and when water infiltration dominates over root uptake, more aerated soil conditions are found near the channels, whereas the inner marsh portions are more oxygenated when plant transpiration balances infiltration from the flooded surface. This inferences clearly highlight how soil and vegetation characteristics (e.g., hydraulic conductivity and vegetation density), which are in turn affected by local elevation and distance from the nearest marsh margin (e.g., Roner et al., 2016), might crucially affect soil aeration. Therefore, oxygen dynamics in marsh soil are quite complex and

may cause difficulties in the detection and interpretation of the relationship between flooding conditions and decomposition processes.

When considering decomposition rate values, k, measured along single transects during different incubation periods, temperature showed to have the strongest influence on decomposition processes, as observed in the analyses presented above, whereas elevation and distance from the marsh edge did not significantly affect decomposition rates along single transects (Figure 7).
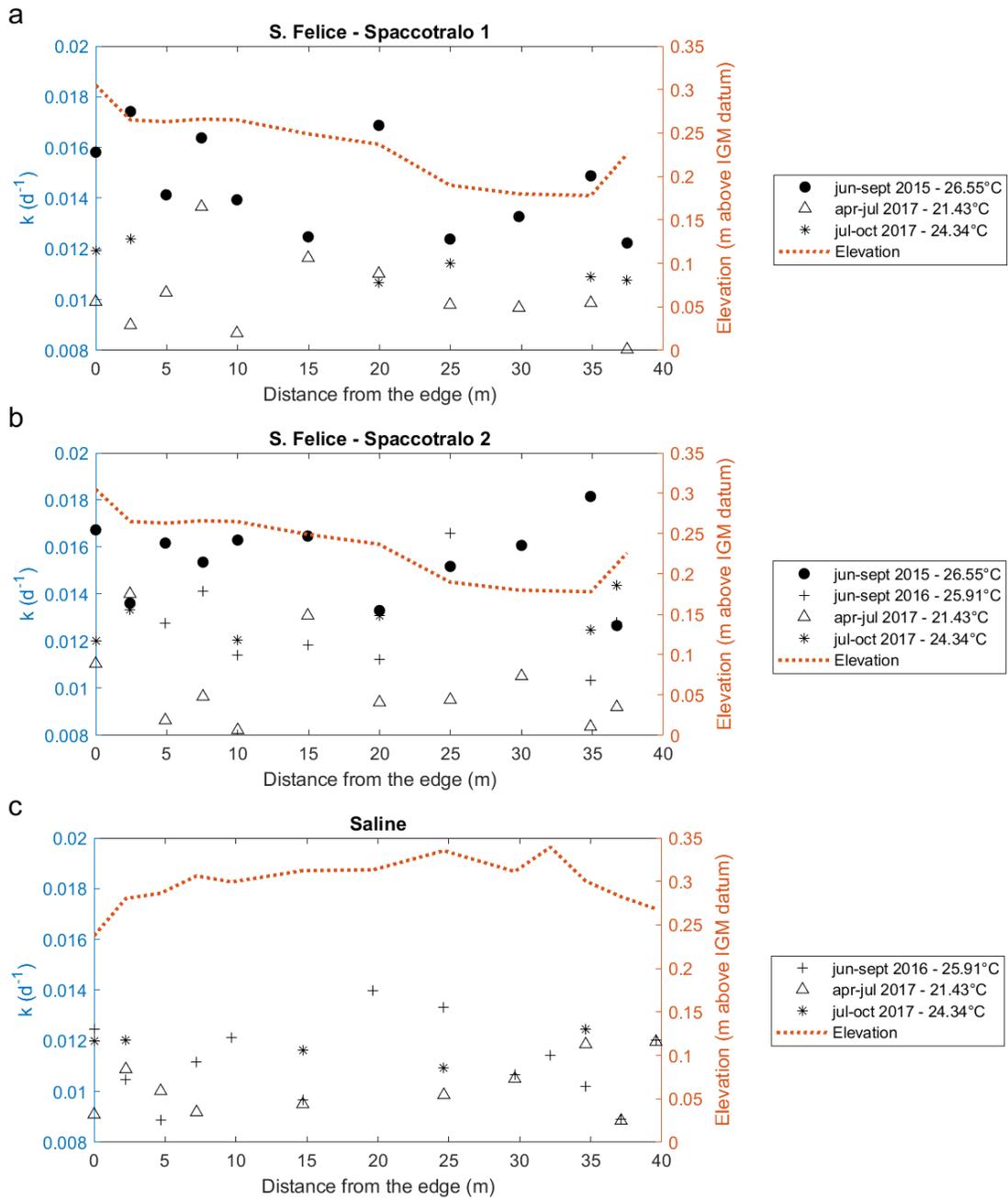
Figure 7. **Decomposition variability at the site scale**. Decomposition rates (k) for different periods with different mean water temperature along single transects, S. Felice – Spaccotralo 1 (a), S. Felice – Spaccotralo 2 (b), Saline (c), with respect to marsh elevation.

4.3 Temperature sensitivity of SOM decomposition

Temperature sensitivity of SOM decomposition is usually described using Arrhenius' (1889) kinetic theory according to which, when substrates are abundant at enzymes reaction sites, decomposition rates increase exponentially with temperature (Davidson & Janssens 2006; Moinet et al. 2020). In addition, the Arrhenius equation suggests that the sensitivity of the reaction rate on temperature increases with increasing availability of the recalcitrant fraction in the substrates (i.e., "intrinsic temperature sensitivity"). However, environmental constraints also influence the observed decomposition response to temperature (i.e., the "apparent temperature sensitivity"), affecting the accessibility to organic carbon substrates (Davidson & Janssens, 2006).

In order to examine the effects of temperature on decomposition processes, we considered the average values of k and S for every surveyed temperature value (Figure 5). Our results suggest an exponential increase of SOM decomposition rates with temperature (Figure 8a) ($k = a\,e^{bT}$), whereas the stabilisation factor, S, is shown to linearly decrease with temperature from from about $S=19\%$ at 21° C to approximately 12% at 27° C.
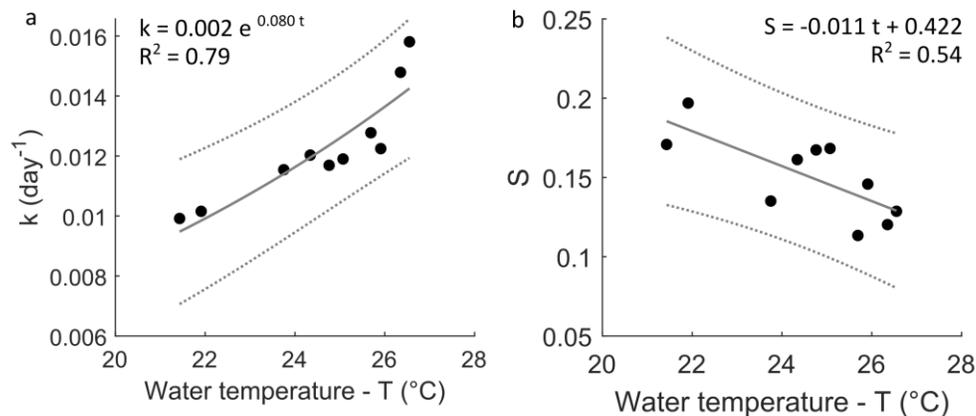

Figure 8. **Correlation between temperature and decomposition metrics**. Exponential regression of decomposition rate (k) (means of the values measured for each incubation period or temperature classes) as a function of the mean water temperature (Coefficients (with 95% confidence bounds): a = 0.002 (0.0002, 0.003), b = 0.08 (0.045, 0.115) (a); and linear regression of the stabilisation factor (S) as a function of the mean water temperature Coefficients (with 95% confidence bounds): p1 = -0.01103 (-0.0193, -0.002763), p2 = 0.422 (0.2182, 0.6257) (b).

In a complex system such as a community of soil organisms, where the total decomposition activity is determined by the combined activity of a wide range

of different organisms that presumably have different individual responses to temperature, the temperature-sensitivity indicator Q_{10} may represent a useful tool to summarize observed responses (Kirschbaum, 1995). Q_{10} is defined as the factor by which a reaction rate increases in response to a 10°C increase in temperature (Davidson & Janssens, 2006) (if $k = a\,e^{bT}$, $Q_{10} = e^{(10\,b)}$).

According to the previously-recalled relation between k and temperature (Fig. 8a), a Q_{10} value of about 2.22 ($Q_{10} = e^{10 \times 0.08} = 2.22$, see Fig. 8 for the value of b=0.08) was computed based on our data (Langley, Johnson, and Koch 2005), which is coherent with the typical values found for reaction rates in biological systems as well as for organic matter decomposition at ambient temperature (Davidson & Janssens, 2006; Kirschbaum, 1995; Singh & Gupta, 1977).

The sensitivity of decomposition on temperature obtained in our analyses is lower than the sensitivity reported for litter bag experiments carried out directly on the soil surface in a rarely flooded salt marsh on the Virginia's coast (Q_{10} = 3.44, (Kirwan & Blum, 2011)). In addition, our Q_{10} value for k agrees with the estimated temperature sensitivities of CO_2 emissions from both freshwater wetland (Q_{10} = 1.3– 2.5) (Inglett et al., 2012) and salt marsh soils (Q_{10} = 1.5– 1.8) (Morris & Whiting, 1986), while appearing slightly larger than those reported by Kirwan et al.(2014) when estimating the range of temperature sensitivity of decomposition rate ($k*$) (Q_{10} = 1.3– 1.5), without accounting for the proportion of recalcitrant and labile material.

Interestingly, when considering the Q_{10} values for the decomposition rates $k*$ of both green tea and rooibos in our tea bag experiments, we obtain Q_{10} = 1.4 and Q_{10} =1.9 for green and rooibos tea (b = 0.033 and 0.066, respectively), respectively, that are closer to those reported by Kirwan et al. (2014). Our analysis on the decay coefficient $k*$ highlighted a lower temperature sensitivity for more labile substrates (e.g., green tea in our TBI analysis) than for recalcitrant substrate (rooibos tea), consistently with the substrate-quality dependence of temperature sensitivity suggested by Arrhenius' (1889) kinetic theory (Davidson & Janssens, 2006).

As to the stabilisation factor, S, we highlight that it declined by about 30% over the observed range of temperatures (21<T<27 °C). Therefore, our results show the dependency of decomposition processes on temperature and, consistently with recent analyses (e.g. Cornwell et al., 2008; Djukic et al., 2018; Stagg et al., 2018), further confirm the key role played by initial litter quality in terms of both chemical and physical composition in driving OM decomposition.

4.4 SOM decomposition at different depths below the marsh surface

At some sites during the 2017 campaign some tea bags were buried at different depths, from the surface to a few tens of centimetres, to analyse depth-related decomposition variability. For 17 burial sites along three transects (S. Felice-Spaccotralo 1 and 2, and Saline) k and S values were measured at the same time

on the marsh surface and at depths of 8, 16, 24, and 40 cm below the surface (Table 2).

Matched pairs	n	Z value	p value
k 0 / -8	17	2.0119	0.0442*
S 0 / -8	17	-1.8699	0.0615
k 0 / -16	17	1.0651	0.2868
S 0 / -16	17	-1.6805	0.0929
k 0 / max depth (-24 or -40)	17	1.9645	0.0495*
S 0 / max depth (-24 or -40)	17	-2.8166	0.0049*
k -8 / -16	17	-0.4971	0.6192
S -8 / -16	17	0.4971	0.6192
k -8 / max depth (-24 or -40)	17	0.3550	0.7226
S -8 / max depth (-24 or -40)	17	-0.3550	0.7226
k -16 / max depth (-24 or -40)	17	1.0651	0.2868
S -16 / max depth (-24 or -40)	17	-1.0951	0.2868

Table 2. **Decomposition variations in matched paired samples at different depth**. Results of the Wilcoxon matched pairs signed rank test on the values of k and S measured at different depths. Asterisks indicate p values being less than the chosen significance level ($p < 0.05$).

The analysis of depth-related decomposition variability (Table 2) showed that decomposition rates measured on the marsh surface are in general significantly different from those measured belowground. As an example, the Wilcoxon matched pairs signed rank test revealed a significant difference in k between the surface and the 8-cm depth ($n = 17$, $Z = 2.0119$, $p=0.0442< 0.05$) and between the surface and the deepest tested layers (depths of 24 and 40 cm) ($n = 17$, $Z = -1.9645$, $p =0.0495< 0.05$), whereas no significant differences were observed between the surface and the 16-cm depth. The difference in decomposition rates, k, among different belowground layers (8, 16, 24, 40 cm depth), on the contrary, were not significant. Differences in stabilization factors, S, turned out to be

significant only between the surface and the deepest layers tested (24 and 40 cm depth) ($n = 17$, $Z = -2.8166$, $p < 0.05$ (0.0049)).
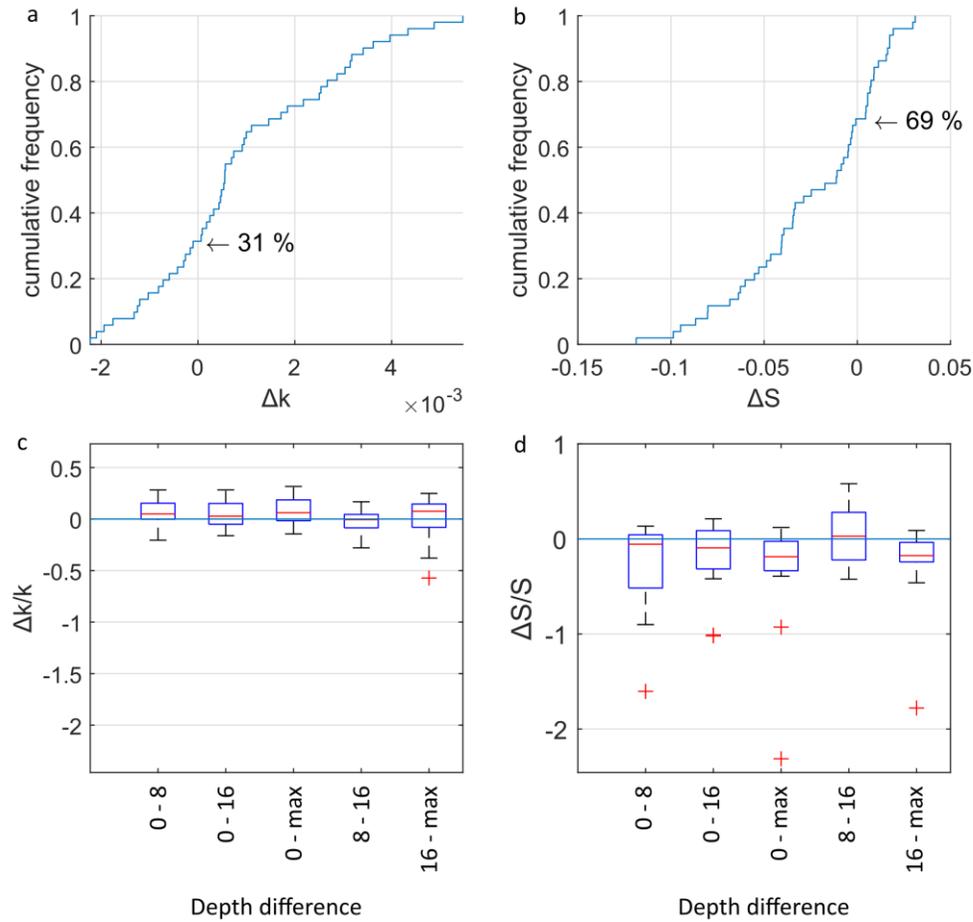

Figure 9. **Differences of decomposition metrics at different depth**. Cumulative distribution function of difference in k (a) and S (b) between the surface and all other deeper layers and box-plots representing the relative difference between k (a) and S (b) values at different depths (The central mark indicates the median, and the bottom and top edges of the box indicate the 25th and 75th percentiles, respectively. Whiskers extend to the most extreme data points not considered outliers and the outliers are plotted individually using the '+' symbol).

For about 70% of burial sites along our study transects, decomposition rates decrease with depth, whereas stabilization factors increase with depth. In general,

deeper soil layers showed lower decomposition rates and higher stabilisation factors compared to more surficial layers (Figure 9 a and b).

The differences between decomposition metrics measured at different depths are in any case limited and in most cases do not exceed 20% (Figure 9 c and d).

In agreement with Yousefi Lalimi et al. (2018), who found that decomposition rates and stabilisation factors of shallower soil layers (3-cm depth) and deeper layers (8-cm depth) were significantly different. Our results suggest that there is a significant difference between the decomposition process on the marsh surface, probably consistent within the first few centimetres of soil, with respect to belowground conditions. Differences in k between different deeper layers within the soil are instead reduced, which may indicate either conditions becoming more uniform or a possible saturation of the effects due to changing controlling factors.

The lower decomposition rates and higher stabilisation factors found in deeper soil layers (Figure 9 a and b) are consistent with the reduced oxygen availability in those layers.

Even though our findings show that deeper soil layers are, on average, characterized by lower decomposition rates and higher stabilisation factors, this difference appears limited (Figure 9 c and d) and decomposition metrics from the study area indicate that the organic matter decay is rapid enough to consume all the labile material before it can be buried and permanently stabilised.

5 Conclusions

To better understand the dynamics of organic matter which contributes to soil formation and carbon sequestration in salt marshes, we analysed decomposition processes in salt-marsh ecosystems in the microtidal lagoon of Venice and investigated how they are influenced by environmental factors.

We carried out decomposition experiments using standardized organic material according to the Tea Bag Index protocol (Keuskamp et al., 2013), focusing only on the initial phases of the decay (i.e., 3 months).

Our results highlight that temperature plays a significant role in OM decomposition and that it is indeed responsible for an increase in the decomposition rate of about 8% per °C. Our results indicate a faster OM decay on the marsh edge and at higher elevations, supporting the idea of slower organic matter degradation towards inner and lower marsh portions (Roner et al., 2016). Moreover, our results highlight how oxygen availability importantly affects decomposition, even if the complexity of soil aeration dynamics prevented the detection of any clear trends in our dataset.

We also suggest that the variability in decomposition metrics, namely the decomposition rate k and the stabilisation factor S, reflects site specific micro-scale variability of the environmental forcing affecting decomposition processes.

Although actual values of S and k for salt-marsh organic matter may differ from those obtained using standard litter, the latter resulted to be comparable with the decay rates calculated using autochthonous plant litter in other studies (e.g., Yousefi Lalimi et al., 2018, Kirwan et al., 2014 and Kirwan & Blum, 2011).

Specifically, the decomposition rates measured in our study display a mean value of 0.012 ± 0.003 day^{-1} (ranging between 0.003 and 0.027 day^{-1}), which would lead to a loss of about two-thirds of the initial organic mass after 90 days. Nevertheless, salt-marsh decomposition rates are confirmed to be some of the lowest with respect to other biomes (see Figure 3).

As to the stabilization processes, our measurements highlight a high variability in stabilization factors: on average 15% of the organic matter was stabilised during the initial stage of decay, with values ranging between 2 and 54 %. Within this scenario, in terms of future climate conditions, the initial litter quality appears to be a primary constraint for the amount of preserved organic matter contributing to carbon sequestration and marsh accretion, as also confirmed by the observed difference in mass loss between green and rooibos tea (mean mass loss of about 70% and 30% in 90 days, respectively). Faster initial decomposition of green tea was expected, and it is due to its higher fraction of water-soluble compounds in contrast to the low content of soluble or hydrolysable compounds in rooibos tea (Keuskamp et al., 2013).

Numerous authors suggested that substrate quality, as a function of chemical and structural characteristics, is a primary control on organic litter decomposition rates, indicating C, N, P, lignin content and their ratios as good predictors for plant decomposability (Enríquez et al., 1993; Kazakou et al., 2009; Li et al., 2012; Prieto et al., 2016; Silver & Miya, 2001). This is confirmed also on a local scale and for coastal marshes (Scarton et al., 2002; Stagg et al., 2018).

Therefore, potential shifts in species relative abundance and primary production in the future caused by climate change and anthropogenic disturbances could have large effects on carbon cycle, affecting litter quality and consequently decomposition rates (Cornelissen et al., 2007; Cornwell et al., 2008; Djukic et al., 2018). This suggests the need to accounting for both direct and indirect effects of climate change as possibly affecting decomposition processes. Hence, we highlight the need for further analyses on autochthonous plant litter dynamics, also on longer time scales, considering their variability.

However, the results of our short-term decomposition experiments cannot be extrapolated to predict long-term behaviour of the decomposition processes, as the Tea Bag Index protocol, by definition, describes early-stage decomposition. The mass loss of the organic litter during early stage decomposition may be more related to the leaching losses than to microbial mineralization of soil organic carbon and long-term decomposition involves different litter components; consequently the drivers of decomposition are likely to vary over longer time scales (Djukic et al., 2018).

Although caution is needed in the interpretation of the decomposition metric measured, our data provide additional insights to improve biogeomorphological model ability to describe marsh response to the effects of climate change and anthropogenic perturbation and further elucidate marsh importance within the global carbon cycle.

Open Research

All data needed to evaluate the conclusions in the paper are available at https://researchdata.cab.unipd.it/id/eprint/762. Meteorological and tide level data for the Venice Lagoon are also freely available at www.comune.venezia.it/content/dati-dalle-stazioni-rilevamento and www.venezia.isprambiente.it/rete-meteo-mareografica.

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