Origin of Organic Carbon in the Topsoil of Wadden Sea Salt Marshes

Running head: Organic carbon origin in salt marshes

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ABSTRACT

Blue carbon ecosystems, including salt marshes, play an important role in the global carbon cycle because of their high efficiency to store soil organic carbon (OC). Few studies focus on the origin of OC stored in salt-marsh soils, which comes from either allochthonous or autochthonous sources. The origin, however, has important implications for carbon crediting approaches because the alternative fate of allochthonous OC (AllOC), i.e. if it had not accumulated in the Blue C ecosystem, is unclear. Here, we assessed the origin of OC in two mainland salt-marsh sites of the European Wadden Sea, analyzing δ^{13}C of topsoil (0-5 cm) samples, freshly deposited sediment (allochthonous source), and of above- and belowground biomass of vegetation (autochthonous sources). We tested for effects of geomorphological factors, including elevation and the distance to sediment sources, and of livestock grazing, as the most important land-use form, on the relative contributions of allochthonous versus autochthonous sources to the topsoil OC stock. A negative effect of distance to the creek on the relative contribution of AllOC was found at only one of the two salt marshes, probably due to differences in micro-topography between the two salt marshes. Additionally, the relative contribution of AllOC increased with increasing distance to the marsh edge in areas without livestock-grazing, while it decreased in grazed areas. Our findings demonstrate that spatial factors such as surface elevation and distance to a sediment source, which have been found to determine the spatial patterns of sediment deposition, also are important factors determining the relative contribution of AllOC to topsoil OC stocks of salt marshes. Furthermore, we provide first evidence that livestock-grazing can reduce the relative contribution of AllOC to the soil OC stock. These findings thereby yield important implications for C crediting and land-use management.

KEY WORDS

stable isotopes, carbon sequestration, livestock grazing, habitat management, Blue carbon, allochthonous, autochthonous, tidal wetland, North Sea

INTRODUCTION

Salt marshes and other tidal wetlands play an important role in climate change mitigation because they are more efficient at storing soil organic carbon (OC) than most terrestrial ecosystems (Chmura et al. 2003, Mcleod et al. 2011). The outstanding capacity of tidal wetlands for long-term carbon (C) sequestration has often been attributed to three main factors, namely high rates of OC input, reduced rates of decomposition, and constant burial of OC with rising sea level (Bridgham et al. 2006, Mcleod et al. 2011). Tidal wetlands are characterized by high rates of autochthonous net primary production, and they are effective in trapping OC from allochthonous marine or riverine sources (Duarte et al. 2013). Moreover, reduced conditions of wetland soils can inhibit microbial metabolism and slow down the decay of organic matter (OM), such that OC can accumulate and remain stable over centuries and millennia in many tidal wetlands (Kirwan & Megonigal 2013). As tidal wetland soils accrete vertically with rising sea level, they do not become C saturated like most terrestrial soils. Rates of C sequestration can therefore be maintained over long time scales, potentially millennia, as evident by deep, C-rich deposits found in tidal-wetland ecosystems worldwide (Mcleod et al. 2011).

The recognition of the important role these coastal ecosystems play in the global C cycle has led to the concept of ‘Blue C’ and a strong interest to include these ecosystems in C crediting programs (Herr et al. 2017). For instance, protection, restoration, or construction of Blue C ecosystems could be credited as greenhouse-gas-offset activities in the context of climate-change policy (Callaway et al. 2012, Needelman et al. 2018). Such measures, however, need to be based on a thorough understanding of the processes driving C sequestration in these ecosystems.

The origin of OC in tidal wetland soils, i.e. allochthonous OC (AllOC) vs. autochthonous OC (AutOC), can have important implications for C crediting and greenhouse-gas-offset activities, because the alternative fate of AllOC, i.e. if it had not accumulated in the tidal wetland, is unclear. For instance, C credits for the sequestration of AllOC are only due in protection, restoration, or construction projects if it would have returned to the atmosphere in the project baseline scenario (Needelman et al. 2018). It is well established that the relative contribution of AllOC vs. AutOC to soil OC stocks can vary considerably across sites and regions (Middelburg et al. 1997, Bouillon et al. 2003). Furthermore, based on studies assessing patterns of C-stable isotope signatures in soils or sedimentary processes within sites, it can be expected that the geomorphology of tidal wetlands and land use play key roles in the relative importance of AllOC vs. AutOC (Ember et al. 1987, Chen et al. 2015, Kelleway et al. 2017, Mueller et al. 2017). Yet, estimates of the relative contributions of AllOC to soil OC stocks derived from such assessments have rarely been conducted.

Numerous studies investigated which geomorphological factors affect the spatial pattern of sediment deposition in tidal wetlands, which is the main pathway for AllOC input. Those factors include surface elevation and distance to sediment sources (i.e. distance to the creek, distance to the marsh edge) (Fagherazzi et al. 2012). In general, lower elevations and closer proximity to the sediment source result in higher sediment deposition (Esselink et al. 1998, Temmerman et al. 2003, Chmura & Hung 2004). Additionally, vegetation height, stem density, and other plant traits are factors known to increase sediment deposition (Morris et al. 2002, Fagherazzi et al. 2012).

Live-stock grazing is a common form of land use or habitat management throughout European salt marshes, but also in other regions, e.g. China and South America (Bakker et al. 2002, Di Bella et al. 2014, Yang et al. 2017). A large number of studies assessed the effects of livestock grazing on soil OC stocks, mineralization, and sequestration in tidal wetlands and produced a wide range of outcomes (Yu & Chmura 2009, Olsen et al. 2011, Elschot et al. 2015, Davidson et al. 2017, Mueller et al. 2017). Because livestock grazing exerts strong control on vegetation dynamics in tidal wetlands, effects on the contribution of AllOC inputs to soil OC stocks can be expected. Specifically, livestock grazing reduces vegetation height (Elschot et al. 2013), and therefore sediment deposition rate might also decrease (Nolte et al. 2015), likely resulting in lower AllOC inputs. Grazing also affects biomass production (Morris & Jensen 1998, Di Bella et al. 2014), which is the source of AutOC. Both reduction in aboveground biomass production (Morris & Jensen 1998) and increases in belowground biomass production (Elschot et al. 2015) under livestock grazing have been reported. In a previous study we hypothesized that the contribution of AllOC could be reduced under high grazing pressures due decreased sediment trapping by shorter vegetation (Mueller et al. 2017). However, a systematic assessment and an understanding of livestock-grazing effects on the relative contribution of AllOC versus AutOC to soil OC stocks in tidal wetlands are yet missing.

The aim of the present study is to identify important spatial factors controlling the relative contributions of AllOC to topsoil (0-5 cm) OC stocks in two salt marshes at the Wadden Sea mainland coast of Germany. δ^{13}C analyses were used to assess the origin of OC, as commonly used in coastal environments (e.g. Thornton & McManus 1994, Kemp et al. 2010, Saintilan et al. 2013). We expect that the relative contribution of AllOC to the soil OC pool is driven by geomorphological factors and additionally mediated by livestock grazing. Specifically, we hypothesize (1) that a higher relative contribution of AllOC would be found in lower elevations within the tidal frame. We hypothesize (2) that the AllOC contribution would decrease with distance to potential sediment sources, namely the distance to creek and the distance to marsh edge. Lastly, we hypothesize (3) that livestock grazing decreases the relative contribution of AllOC.

MATERIALS AND METHODS

Study sites and sampling design

The study was conducted from Dec 2014 to Sep 2015 in two salt marshes at the mainland coast of the Schleswig-Holstein Wadden Sea National Park, Germany (Fig. 1 A). The salt marshes within the National Park cover an area of ~130 km², approximately half of which is used for livestock grazing (Stock et al. 2005, Esselink et al. 2017). Both study sites, Dieksanderkoog (DSK) and Sönke-Nissen-Koog (SNK), are minerogenic, shallow depositional salt marshes, exposed to tidal amplitudes of 3.0-3.4 m at a diurnal frequency. Soils in both sites have OM contents <15% and are dominated by grain-sizes <63 µm (>70% silts and clays)(Mueller et al. 2019). Flooding of the extensive high-marsh platforms, that this study is restricted to, only occurs during storm events predominantly in winter (Müller et al. 2013a, Butzeck et al. 2015). In both sites, the presence of a rectangular network of creeks, ditches and levees reveal the anthropogenic origin of the salt marsh during land reclamation in the beginning of the 20th century (Müller et al. 2013b). The DSK (53°58′N, 8°53′E) is located in the southern part of the National Park at the mouth of the Elbe Estuary, while the SNK (54°38′N. 8°50′E) is situated in the north, ca. 35 km south of the Danish border (Fig. 1). Both sites were entirely grazed by sheep until 1988 and 1992 (SNK and DSK, respectively), when grazing was abandoned and only maintained at high stocking densities of >10 sheep ha^{-1} until today in distinct areas of the two sites for experimental purposes (Stock et al. 2005, Mueller et al. 2017). The grazed treatment is dominated by *Festuca rubra*, *Elymus athericus*, and *Artemisia maritima* at DSK, and by *Puccinellia maritima*, *Festuca rubra*, and *Elymus athericus* at SNK. The ungrazed treatments are dominated by *Elymus athericus* at both sites.

Grazed and ungrazed treatments are located next to each other and separated by a straight main creek. In each treatment, sampling points were placed along short and long transects (Fig 1. B). The long transects covered a distance of 620 m (SNK) and 730 m (DSK) along the main creek and consisted of five sampling points, starting at the seaward edge of what is considered here as the anthropogenic high-marsh platform (distance to marsh edge = 0 m). The long transects kept an almost constant distance to the main creek of 54 m at SNK and 62 m at DSK. Short transects ran perpendicularly to the main creek and consisted of five points with different distances to the main creek (3 - 104 m at SNK; 2 - 107 m at DSK). The central points of the short transects were also part of the long transects (Fig.1). This sampling design resulted in N = 13 sampling points per treatment and a total of N = 52 sampling points for both marsh sites. Surface elevation relative to the German ordnance datum (NHN = Normalhöhennull) of sampling points was measured using a laser leveling device (Trimble, Sunnyvale, California, USA) and a nearby fixed benchmark with known elevation.

Sample collection

We used C-stable isotope analysis to distinguish between AllOC and AutOC. To assess the δ^{13}C of the AllOC source, freshly deposited sediments were collected using circular sediment traps (Temmerman et al. 2003, Nolte et al. 2013a, 2019). The sediment traps were built of plastic plates with an internal diameter of 19 cm and a rim of 3 cm, and were equipped with a floatable lid to protect the deposited sediment in the trap from disturbances (Temmerman et al. 2003). Traps were fixed to the marsh surface with a plastic stick (Butzeck et al. 2015). Sediment traps were sampled within 24 h after two storm events during winter 2014/15. The high-marsh platform is only flooded during storm-induced high tides, so that sediment and AllOC deposition is restricted to these events (Müller et al. 2013a, Butzeck et al. 2015). As we assumed the δ^{13}C of the freshly deposited sediment to be similar throughout the marsh, we only deployed sediment traps at five sampling points along the long transect and at two sampling points nearest to the creek in the two short transects in each treatment and site (Fig. 1), resulting in the total number of 28 sediment traps. In the following, we will only refer to the data of one sampling event in Dec 2014, when the majority of traps (27 out of 28) contained deposited material, after ensuring that no significant differences in C-stable isotope signatures exist between sampling events.

Above- and belowground plant biomass, as AutOC source, was sampled at all sampling points at the end of the growing season 2015. Aboveground biomass was harvested at each sampling position in an area of 100 cm^2. Belowground biomass of the uppermost (5 cm) soil layer was collected using a soil corer (Ø 2.5 cm). Dual cores were taken at each sampling position and samples were subsequently pooled. All samples were stored at -20^0C until processing for further analysis.

To assess the $\delta^{13}C$ of soil OC, soil samples of the uppermost 5 cm soil layer were collected at all sampling positions using a soil corer (Ø 2.5 cm) in Dec 2014. Our study investigated the origin of OC only in the uppermost 5 cm of the soil, because belowground biomass is usually concentrated at this depth in mainland high marshes of the Wadden Sea (Bartholdy et al. 2014, Redelstein et al. 2018). Additionally, down-core ^{13}C fractionation through repeated microbial cycling of OC and preferential substrate utilization make conclusions concerning the OC origin increasingly difficult with soil depth (Mueller et al. 2019). Samples were transferred to the laboratory and stored at -20°C until processing.

Sample processing and analysis

Deposited sediment and soil samples were dried at 60°C until no further weight loss was observed. Plant materials and potential other coarse organic debris was removed by passing the sample through a 2-mm sieve. Samples were ground and homogenized using pestle and mortar. Sub-samples (1 g) were treated with 10% hydrochloric acid to remove carbonates and again dried at 60°C. Biomass samples were cleaned using tap water and given a final rinse with deionized water before drying at 60°C. Dry biomass samples were ground and homogenized in a ball mill (Retsch, Haan, Germany). $\delta^{13}C$ of dried and homogenized bulk soil OM, deposited sediment OM, and fresh above- and belowground biomass were determined using an isotope ratio mass spectrometer (Nu Horizon, Nu Instruments, Wrexham, UK). Samples were analyzed in tandem with both laboratory (BBOT 2,5-Bis-(5-tert-butyl-2-benzo-oxazol-2-yl) thiophene) and international standards (IAEA-600 Caffeine). The precision of the isotopic analysis was < 0.1‰. The isotopic compositions of all samples are reported using the standard δ-notation versus Vienna PeeDee Belemnite (VPDB) as parts per thousand (‰).

The relative proportions of the AllOC and AutOC were determined by applying a two-end-member mixing model based on the stable isotope composition of OC (e.g. Hedges et al. 1988, Belicka and Harvey 2009):

$$f_{Al}(\%) = \frac{\delta^{13}C_{Soil} - \delta^{13}C_{Au}}{\delta^{13}C_{Al} - \delta^{13}C_{Au}} \qquad (1)$$

where: f_{Al} (%) is the percentage contribution of the Al OC in soil; $\delta^{13}C_{Soil}$ is $\delta^{13}C$ measured in the soil; $\delta^{13}C_{Au}$ is $\delta^{13}C$ of the AutOC source (plant biomass); and $\delta^{13}C_{Al}$ is $\delta^{13}C$ of Al OC.

The calculated contributions of AllOC vs. AutOC sources depend on the type of plant biomass (i.e. above- vs. belowground biomass) considered in the mixing-model calculations. As the contributions of above- vs. belowground plant biomass to the soil OM pool were unknown, we calculated f_{Al} (%) under the assumption of three different end-member terms for Au $\delta^{13}C$: (1) $\delta^{13}C$ of the aboveground biomass (Model A), (2) $\delta^{13}C$ of the belowground biomass (Model B), and (3) the calculated $\delta^{13}C$ of a 1:1 mixed contribution of above- and belowground biomass (Model M).

Statistical analyses

Two-way ANOVAs were used to test for differences in the isotopic composition of sediment and soil between sites and treatments. To test if $\delta^{13}C$ of AllOC in deposited sediment differs in response to distance to the marsh edge, linear regressions were used separately for each site. To test if $\delta^{13}C$ of AllOC deposited in sediment traps positioned close to the creek differ from those positioned far from the creek, one-way ANOVAs were used separately for each site. Three-way ANOVA was used to test for the effects of site, treatment, and type of plant tissue (above- vs. belowground biomass) on plant $\delta^{13}C$, and subsequent two-way ANOVAs were conducted to test for the effects of treatment and site on the $\delta^{13}C$ of above- and belowground biomass separately. Tukey's HSD tests were used for pairwise comparisons. Normal distribution of residuals (as checked visually) and equal sample sizes across groups assured robustness for parametric testing (McGuinness 2002).

ANCOVA was conducted to test for effects of site, treatment, distance to marsh edge, distance to creek, and relative elevation (elevation in comparison to mean surface elevation at each site) on the relative contribution of AllOC to the soil. Only pairwise interactions of factors were considered in the models. As model simplification is an essential part of ANCOVA designs, the most insignificant parameters were dropped step by step, and as few parameters as possible were kept in the model (Crawley 2005). The more complex models were retained only if the p-value (ANOVA based) comparing the two models was < 0.05 (Crawley 2005). To exclude that identified effects on the contribution of AllOC are artifacts driven by spatial variability in the plant isotopic signature, we additionally conducted the same ANCOVA procedures to test for effects of spatial factors and grazing on the autochthonous $\delta^{13}C$ end members (i.e. aboveground, belowground, mixed). All analyses were carried out using the software package 'R' version 3.3.1 (The R Foundation for Statistical Computing 2016).

RESULTS

$\delta^{13}C$ of AllOC, AutOC, and soil samples

$\delta^{13}C$ of AllOC in deposited sediment differed significantly between sites ($F_{1,23} = 88.6$, $p < 0.0001$). AllOC was more depleted in $\delta^{13}C$ at DSK (-24.22‰ ± 0.35‰) vs. SNK (-23.10‰ ± 0.25‰) (Table 1). Within sites, no significant differences in $\delta^{13}C$ of the AllOC were detected between grazed and ungrazed treatments (Table 1). There was no significant interaction effect of site and treatment on the $\delta^{13}C$ of AllOC ($F_{1,23} = 0.7$, $p > 0.4$). $\delta^{13}C$ of AllOC did not differ in response to distance to the marsh edge (in each site: $R^2 < 0.25$, $p > 0.1$). $\delta^{13}C$ of AllOC in traps positioned close to the creek did not differ from those positioned far from the creek (DSK: $F_{1,6} = 2.2$, $p > 0.1$; SNK: $F_{1,6} = 1.9$, $p > 0.2$). Therefore, the mean $\delta^{13}C$ of each site was chosen for $\delta^{13}C_{Al}$ in Equation 1.

The $\delta^{13}C$ values of AutOC differed between sites ($F_{1,93} = 17.1$, $p < 0.0001$), treatments ($F_{1,93} = 11.6$, $p < 0.001$), and type of plant tissue, i.e. above- vs. belowground biomass ($F_{1,93} = 5.9$, $p < 0.05$). There was a significant interaction effect of treatment and type of plant tissue on $\delta^{13}C$ of AuOC ($F_{1,93} = 4.0$, $p < 0.05$). Subsequent two-way ANOVAs showed the effects of site and treatment on $\delta^{13}C$ of aboveground biomass, belowground biomass and the 1:1 mixed above- and belowground biomass (Table 1). The aboveground biomass $\delta^{13}C$ values were significantly different between sites ($F_{1,47} = 11.5$, $p < 0.005$), with $\delta^{13}C$ being more depleted in DSK (-27.72‰ ± 0.74‰) vs. SNK (-26.65‰ ± 1.38‰) (Table 1). Treatment had no effect on $\delta^{13}C$ of aboveground biomass, and there was also no interaction of site and treatment effect on the $\delta^{13}C$ of aboveground biomass (Table 1). $\delta^{13}C$ values of belowground biomass were affected significantly by site ($F_{1,46} = 6.0$, $p < 0.05$), being more depleted in DSK (-27.00‰ ± 1.05‰) vs. SNK (-26.32‰ ± 1.24‰) (Table 1). $\delta^{13}C$ of belowground biomass were constantly more depleted under grazing ($F_{1,46} = 16.5$, $p < 0.001$) at both sites. The interaction of site and treatment had no effect on belowground biomass $\delta^{13}C$. Similarly, the 1:1 mixed biomass $\delta^{13}C$ was affected significantly by site ($F_{1,47} = 15.8$, $p < 0.0005$) and treatment ($F_{1,47} = 9.7$, $p < 0.01$), but not by the interaction of site and treatment. These differences in $\delta^{13}C$ between above- and belowground biomass, treatments, and sites did not allow using any sort of mean $\delta^{13}C$ value for the autochtonous end-member term in mixing models. Instead, we used the specific $\delta^{13}C$ values of above-, belowground, and mixed biomass of each sampling point for the respective mixing-model calculations (Equation 1).

Soil OC had $\delta^{13}C$ values varying from -28.00‰ to -23.24‰ and differed significantly by site ($F_{1,48} = 34.7$, $p < 0.001$). $\delta^{13}C$ of DSK soil OC (-26.75‰ ± 0.35 ‰) was more depleted than SNK soil OC (-25.61‰ ± 0.85 ‰). Treatments had an effect on soil OC $\delta^{13}C$, ($F_{1,48} = 10.4$, $p < 0.01$), with more depleted ^{13}C under grazing (-26.49‰ ± 0.95 ‰) compared to ungrazed treatments (-25.87‰ ± 0.82 ‰) (Table 1). There was no significant interaction effect between site and treatment on soil OC $\delta^{13}C$ values (Table 1).

Relative contribution of AllOC in salt-marsh topsoils

The three mixing models in which different AutOC end-member assumptions (only aboveground plant biomass (A), only belowground plant biomass (B), or 1:1 mixed plant biomass (M)) were used to calculate contributions of AllOC to the salt-marsh topsoil OC yielded different results (Fig. 2). Depending on the model used, AllOC contributions in grazed treatments ranged from 17.72 ± 3.85 to 23.64 ± 4.84 (%). In comparison, a higher range was found in ungrazed treatments (from 11.79 ± 4.95 to 38.99 ± 5.31(%)). Here, we found that a mixing model using the aboveground $\delta^{13}C$ resulted in much higher contributions of AllOC to the topsoil OC stock compared to using the belowground $\delta^{13}C$ (Fig. 2).

The ANCOVA results for the three mixing models, which were based on different autochthonous OC end-member assumptions (see above) also differed (Table 2). For further interpretation, we therefore considered only those effects as robust which were found to be significant in at least two models (Table 2).The interaction effect between site and distance to the creek was found to be significant in Model A and Model M (Table 2). In DSK, we found the highest AllOC contributions close to the creek. With increasing distance to the creek, there was a steep drop until a more or less stable value was reached (Fig. 3 A). In contrast, the contribution of AllOC in SNK showed a different pattern and remained constant with increasing distance to the creek (Fig. 3 A). The interaction between treatment and distance to the marsh edge also had significant effects on the contribution of AllOC in Model A and Model M (Table 2). Close to the marsh edge (0 to 300 m), the percentages of AllOC contribution were quite similar between treatments (Fig. 4 A). In the area of greater distance to the marsh edge, however, we found opposite patterns for the two treatments. Here, the percentage of AllOC increased with increasing distance to the marsh edge in ungrazed treatments, while it decreased in grazed treatments (Fig. 4 A).

ANCOVAs assessing the effects of geomorphological factors and grazing on the autochthonous δ^{13}C end members (i.e. aboveground, belowground, mixed biomass) showed neither interaction effects of distance to the marsh edge and treatment, nor of site and distance to the creek, excluding that the identified effects on the AllOC contribution to the soil are artefacts driven by spatial variability in plant δ^{13}C (Table A1).

DISCUSSION

The present study assessed the relative contributions of AllOC to topsoil OC stocks in two salt-marsh sites of the European Wadden Sea. A large number of studies on the importance of AllOC in marsh soils have been performed (e.g. Boschker et al. 1999, Tanner et al. 2010, Saintilan et al. 2013, Chen et al. 2015, Van de Broek et al. 2018). However, estimates of the relative contribution of AllOC vs. AutOC to OC stocks have rarely been provided. This is possibly due to large uncertainties associated with the application of two-end-member mixing models, which were also encountered in the present study (see discussed below in 'Methodological considerations'). For instance, mean AllOC contributions to topsoil OC stocks of the high-marsh platforms ranged between 18 and 31% of total soil OC depending on autochthonous δ^{13}C end-member assumptions. The central aim of our investigation was therefore not to provide accurate budgets of AllOC vs. AutOC contributions, but to identify important spatial factors influencing the balance of the two sources. Specifically, we hypothesized that surface elevation, distance to sediment sources, and livestock grazing negatively affect the relative contribution of AllOC to the soil OC stock. Our findings can provide partial support for these hypotheses because complex interactions between the assessed factors existed and seem to exert important control on the distribution pattern of AllOC.

Relative elevation as a single factor did not affect the relative contribution of AllOC to the topsoil. We did, however, identify a negative effect of distance to the creek on the relative contribution of AllOC to the topsoil. This effect was only found at DSK and not at SNK, which we attribute to differences in relative elevation patterns within sites, and more specifically, in patterns of levee formation along the main creek (Fig. 3 B). At SNK, sampling points closest to the main creek are characterized by the highest relative elevation. We argue that this natural levee along the creek restricts inundation of the marsh platform until tidal heights exceed the levee elevation, resulting in similar inundation frequencies and AllOC inputs across the marsh platform (Fig. 3). At DSK, by contrast, sampling points closest to the creek are lower than subsequent points with larger distance to the creek, leading to highest AllOC inputs close to the creek (Fig. 3). As previously hypothesized (Haines 1976, Ember et al. 1987, Middelburg et al. 1997), our findings provide evidence that geomorphological factors such as surface elevation and distance to the creek, which determine the spatial patterns of sediment deposition (Esselink et al. 1998, Temmerman et al. 2003, Chmura & Hung 2004), also are important factors determining the relative contribution of AllOC to the topsoil OC stocks of salt marshes. Yet, our data do not allow assessing if variability in AuOC input contributed to this finding. For instance, biomass production in salt marshes is also strongly controlled by geomorphological factors, such as elevation, affecting both hydrology and nutrient supply (Morris et al. 2002, Kirwan & Guntenspergen 2012).

Besides distance to the creek, distance to the marsh edge is a second parameter describing the proximity of a given point to a potential sediment and thus AllOC source. We indeed demonstrate a significant effect of distance to the marsh edge. This effect, however, differed significantly between grazed and ungrazed treatments (Table 2). Specifically, our data show increasing relative contributions of AllOC with distance to the marsh edge in ungrazed treatments, whereas the opposite pattern was found in the grazed treatments (Fig. 4 A). We argue that the unexpected increase of the AllOC contribution with distance to the marsh edge in ungrazed treatments can be explained by elevational patterns of the marsh platform that are typically found across Wadden Sea salt marshes and elsewhere. Landward decreases in elevation often result from ditching, diking, and grazing processes in salt marshes (Stock 2011, Müller-Navarra et al. 2016, Esselink et al. 2017) and were also found in the two sites investigated here (Fig, 4 B). As a consequence, landward areas of the marsh platform are flooded first and potentially more frequently, thus explaining higher relative contributions of AllOC in the landward ungrazed treatments.

The mechanisms causing the opposite effect of distance to marsh edge on the relative contribution of AllOC to the topsoil in grazed treatments is unknown. However, we hypothesize that they relate to pronounced differences in grazing pressure between landward and seaward locations (Kiehl et al. 2001, Nolte et al. 2013b, Mueller et al. 2017). Because livestock tends to remain close to the freshwater source near the seawall (Kiehl et al. 2001), grazing pressure increases with distance to the marsh edge, which is also reflected in decreasing vegetation height and increasing soil bulk density with increasing distance to the marsh edge in our study sites (Nolte 2014, Mueller et al. 2017). At least three non-exclusive mechanisms, supported by literature, could explain lower relative AllOC contributions at high grazing pressures. First, grazing-induced reductions in vegetation height could lead to lower plant-mediated sediment trapping (Morris et al. 2002, Fagherazzi et al. 2012) and thus AllOC input in (Yang et al. 2008, Mueller et al. 2017). Second, livestock grazing is known to increase belowground AutOC inputs through higher root production (Elschot et al. 2015), which would translate into lower relative contributions of AllOC. Third, grazing could lead to a more effective preservation of AutOC in the soil, thereby decreasing the relative contribution of AllOC. That is, grazing-induced soil compaction is known to lower soil oxygen availability and thus reduce microbial activity (Elschot et al. 2015, Mueller et al. 2017). However, recent studies from the North Sea region suggest AllOC inputs are highly resistant to decay, being old-aged materials that stabilized in the marine environment before entering the marsh OC pool (Van de Broek et al. 2018, Mueller et al. 2019). It therefore seems likely that primarily the decay of autochthonous OM is susceptible to grazing effects on oxygen availability and microbial activity.

Although our findings cannot identify the mechanism(s) responsible for the observed grazing effect, they yield important implications for ecosystem management and C crediting. Recent meta-analyses and large-scale studies suggest livestock grazing has no effect on soil OC stocks of salt marshes (Davidson et al. 2017, Ford et al. 2019). Our study provides first evidence of grazing effects on the balance between allochthonous and autochthonous soil OC. Because it is uncertain if C credits are due for the sequestration of AllOC, livestock grazing may actually increase the C value of salt-marsh area, by reducing the relative contribution of AllOC to the soil OC stock. However, there are important caveats concerning these implications; our study did not quantify absolute rates of AllOC vs. AutOC input and accumulation, but only reports on the relative contributions of the two sources to the soil OC stock. Yet, the majority of studies concerned with grazing effects on salt-marsh C dynamics are likewise restricted to OC stock assessments, but did not quantify rates of sequestration (Davidson et al. 2017, but see Elschot et al. 2015). In addition, recent studies provide evidence of a more effective preservation of allochthonous OM inputs in marsh soils than in situ produced OM, leading to an increasing relative contribution of AllOC vs. AutOC with soil depth or time in NW European salt marshes (Van de Broek et al. 2018, Mueller et al. 2019). Future research therefore needs to assess whether the here identified grazing effects on the balance between AllOC and AutOC remain with increasing soil depth and are thus relevant for considerations on long-term C dynamics.

Methodological considerations

Large differences were found in the estimates of AllOC contribution when the three mixing model approaches based on different plant δ^{13}C end-members assumptions were compared, particularly in the ungrazed treatments (Fig. 2). We therefore stress the importance to consider differences in the isotopic composition of different plant tissues in mixing-model approaches used to calculate the relative contributions of AllOC vs. AutOC, which is surprisingly left unconsidered in many studies (but see Kelleway et al. 2018). In the present study, we found large differences in $\delta^{13}C$ between above- and belowground biomass (Table 1). Because the relative contribution of above- vs. belowground biomass to the top soil is unknown, also the absolute values presented here need to be considered with caution. Depending on the end-member assumptions used (i.e. Model A vs. B vs. M), calculated AllOC contributions to the topsoil can be as low as 0% in some sampling points (Fig. 4 A). This seems unrealistically low, and may point to the fact that the actual ratio of above- to belowground contributions to the soil OC pool diverge from the end-member assumption. For instance, it is reasonable to assume small aboveground and large belowground contributions under grazing, considering the negligible aboveground litter accumulation (Mueller et al. 2017). Indeed, Model B (assuming no aboveground contributions) yields more realistic AllOC contributions of 4% for the sampling points yielding a 0% in Model M (Fig. 4 A).

Unless relative contributions of different plant tissues to the soil OC pool are known, simple two-end-member mixing models can only yield an approximation of AllOC vs. AutOC contributions to soil OC stocks. The main goal of this study was therefore not to calculate precise budgets of AllOC vs. AutOC inputs, but to identify important factors controlling their relative distributions. Here, we used three different assumptions for our autochthonous end members to assess the robustness of the results obtained. Above, we only discussed effects that were significant in at least two of the three models tested. Additionally, however, there were other significant effects that were only detected by one of the three models, which provide additional support for the factors identified to be important and discussed above. That is, negative effects of grazing, distance to the creek, and relative elevation on the relative contribution of AllOC to the top soil were additionally detected by Models A and M (Table 1). Furthermore, a significant interaction of grazing and relative elevation was detected by Model B, supporting the interpretation that the interaction effect of grazing and distance to the marsh edge is mediated by differences in surface elevation.

In order to exclude artifacts caused by spatial variability in δ^{13}C of plant biomass (i.e. our autochthonous δ^{13}C end members), we also tested for effects of site, treatment, distance to the marsh edge, distance to the creek, and relative elevation on the autochthonous δ^{13}C end members used. We found neither interaction effects of distance to marsh edge and treatment, nor of site and distance to creek on the autochthonous δ^{13}C end member, excluding that the identified interaction effects on the AllOC contribution are artifacts driven by spatial variability in the plant δ^{13}C (Table A1).We argue that such sensitivity analyses are crucial to assess the reliability of conclusions derived from stable-isotope mixing-model approaches.

Conclusions and perspective

The present study partly supported previous research showing that more AllOC is found closer to the sediment sources and in lower elevations (Middelburg et al. 1997, Spohn et al. 2013, Hansen et al. 2017, Yuan et al. 2017). However, while previous studies have shown that the contribution of AllOC to soil OC varies among different zones of tidal marshes (Spohn et al. 2013) or across sites and regions (Middelburg et al. 1997, Hansen et al. 2017, Yuan et al. 2017), our study is the first to evaluate geomorphology and land-use effects on the small scale variability in the relative contribution of AllOC to soil OC stocks. Our findings demonstrate that spatial factors such as surface elevation and distance to a sediment source, which have been found to determine the spatial patterns of sediment deposition (Esselink et al. 1998, Temmerman et al. 2003, Chmura & Hung 2004), also are important factors determining the relative contribution of AllOC to the topsoil OC stocks of salt marshes. Furthermore, we provide first evidence that livestock-grazing can reduce the relative contribution of AllOC to the soil OC stock. These findings could yield important implications for C crediting and land-use management. Future research is required to quantify absolute rates of AllOC vs. AutOC inputs and to assess whether the here identified effects on the balance between AllOC and AutOC remain with increasing soil depth and are thus relevant for considerations on long-term C dynamics.

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FIGURES

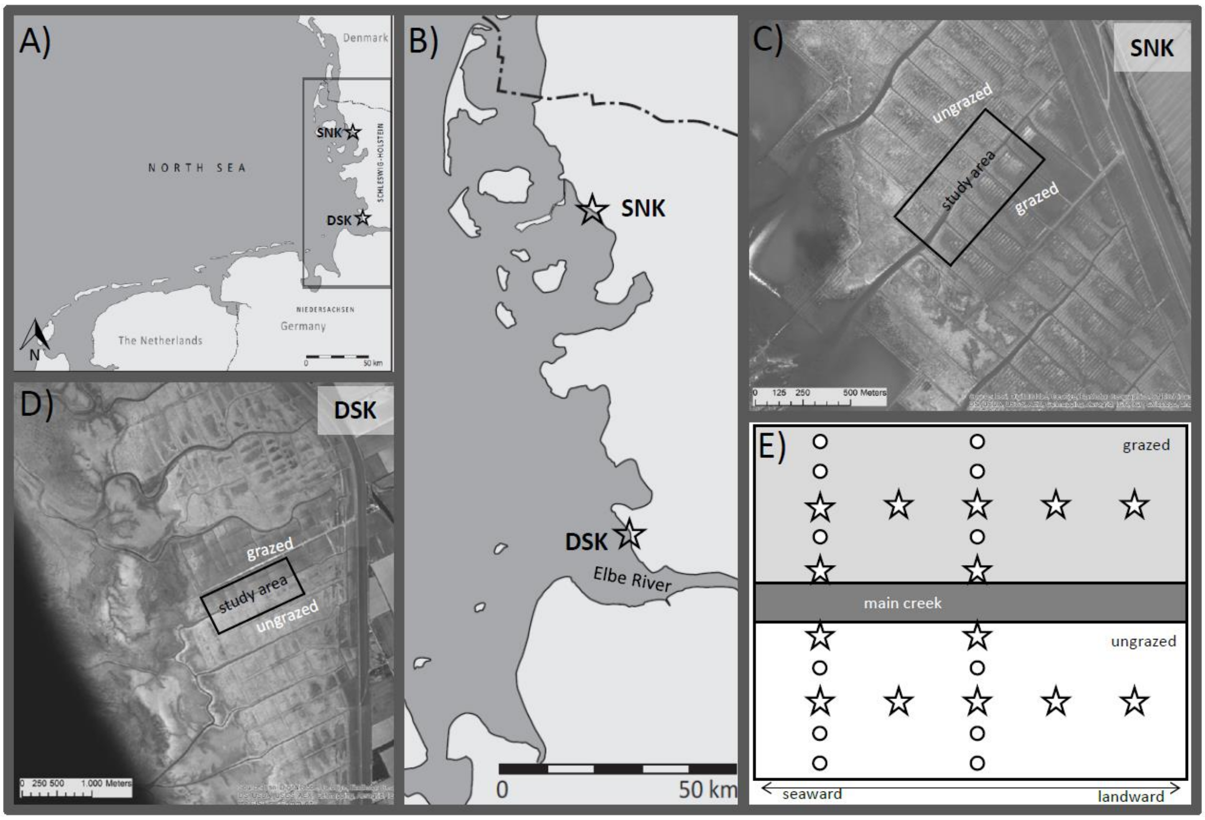

Figure 1 (A +B) Location of the study sites Sönke-Nissen-Koog (SNK) and Dieksanderkoog (DSK) within the Wadden Sea area. **(C + D)** Aerial photos of the study sites. **(E)** Sampling design: sampling points were organized along short transects (distance to the creek) and long transects (distance to the edge of the anthropogenic high-marsh platform) in grazed vs. ungrazed treatments. Soil and biomass samples were collected at all points ,while deposited sediment samples were only collected at points marked with star symbols. Aaerial photos source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus CS USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community.

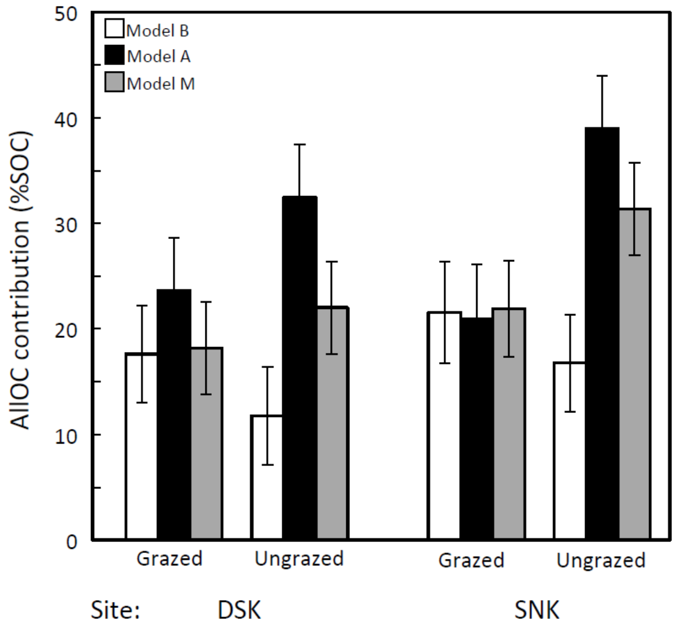

Figure 2 Allochthonous organic carbon (AllOC) contribution in percent of soil organic carbon (%SOC) in the topsoil of grazed und ungrazed treatments of two Wadden Sea salt-marsh sites, Dieksanderkoog (DSK) and Sönke-Nissen-Koog (SNK). Values presented are based on mixing-model calculations using three different end-member assumptions for the $\delta^{13}C$ of autochthonous organic carbon: **Model B** ($\delta^{13}C$ of the belowground biomass), **Model A** ($\delta^{13}C$ of the aboveground biomass), **Model M** (the calculated $\delta^{13}C$ of a 1:1 mixed contribution of aboveground and belowground biomass). Values are means ± SE.

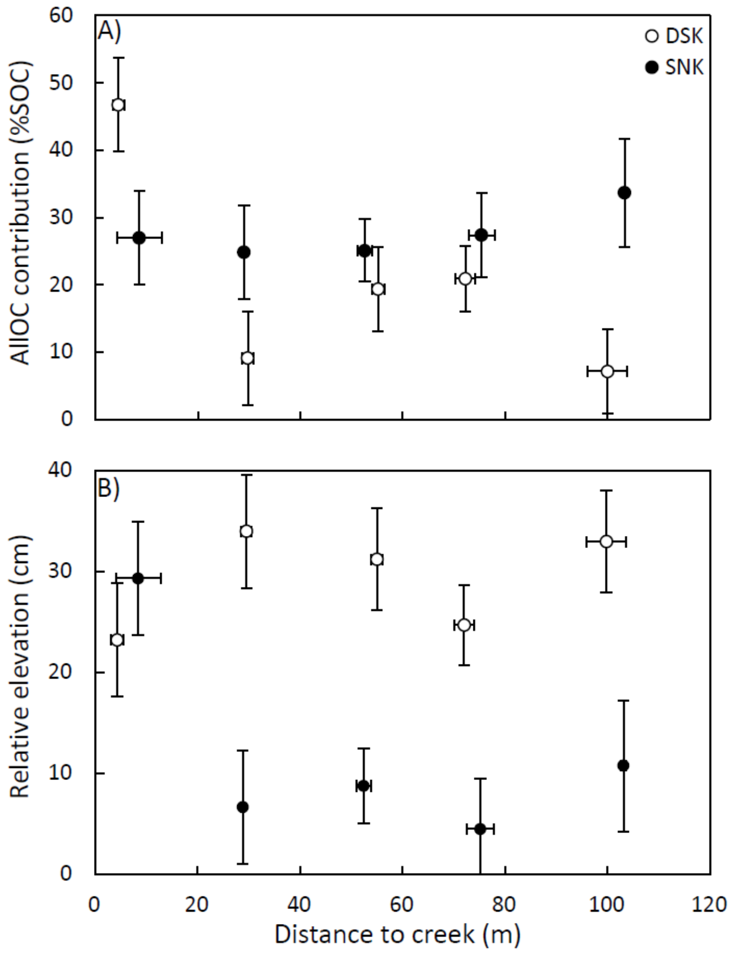

Figure 3 (A) Allochthonous organic carbon (AllOC) contribution [percentage of soil organic carbon (%SOC)] in relation to distance to the creek in two Wadden Sea salt-marsh sites, Dieksanderkoog (DSK) and Sönke-Nissen-Koog (SNK). Values are based on Model M (i.e. the calculated $\delta^{13}C$ of a 1:1 mixed contribution of aboveground and belowground biomass was used for the $\delta^{13}C$ of autochthonous organic carbon in mixing-model calculations). **(B)** Relative elevation of the sampling points in relation to distance to the creek in DSK and SNK. Values are means ± SE.

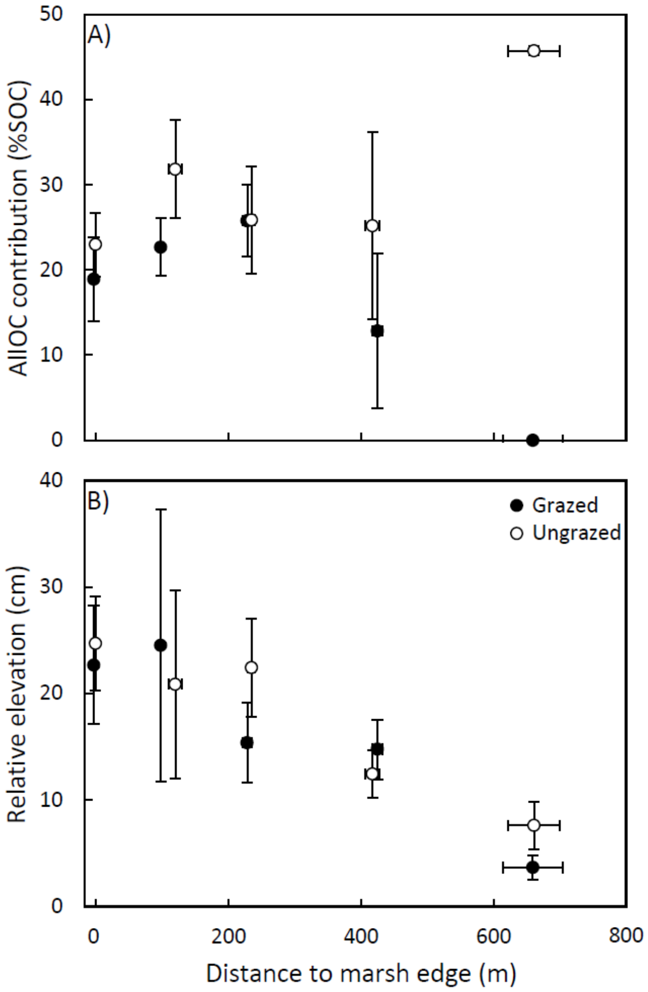

Figure 4 (A) Allochthonous organic carbon (AllOC) contribution [percentage of soil organic carbon (%SOC)] in relation to distance to the marsh edge in grazed vs. ungrazed treatments of two Wadden Sea salt-marsh sites. **(B)** Relative elevation of the sampling points in relation to distance to the marsh edge in. Values are means ± SE, pooled by site.

TABLES

Table 1 δ^{13}C of allochthonous and autochthonous OC sources (AllOC, AutOC) and topsoil samples in grazed und ungrazed treatments of two Wadden Sea salt-marsh sites. Values are means ± SD given in δ-notation versus Vienna PeeDee Belemnite (‰). Values not connected by the same letter within one row are significantly different at $p < 0.05$ based on Tukey's HSD tests.

	Dieksanderkoog (DSK)		Sönke-Nissen-Koog (SNK)	
Sample material	Grazed	Ungrazed	Grazed	Ungrazed
Deposited sediment (AllOC)	-24.29^{a} ± 0.42	-24.14^{a} ± 0.26	-23.08^{b} ± 0.20	-23.12^{b} ± 0.31
Plant biomass (AutOC)				
Aboveground	-27.81^{a} ± 0.74	$-27.62^{a,b}$ ± 0.76	$-26.86^{a,b}$ ± 1.16	-26.45^{b} ± 1.58
Belowground	-27.38^{a} ± 1.16	$-26.60^{a,b}$ ± 0.77	-27.10^{a} ± 1.05	-25.60^{b} ± 0.95
1:1 mixed	-27.60^{a} ± 0.98	-27.11^{a} ± 0.91	-26.97^{a} ± 1.09	-26.03^{b} ± 1.35
Topsoil	-27.04^{a} ± 0.57	$-26.46^{a,b}$ ± 0.59	-25.94^{b} ± 0.96	-25.28^{b} ± 0.58

Table 2 Results of ANCOVA analyses testing for effects of single and interacting factors on the allochthonous organic carbon contribution (percentage of soil organic carbon) to the topsoil of two Wadden Sea salt-marsh sites. ANCOVA analyses were run using three different end-member assumptions for the δ^{13}C of autochthonous organic carbon in mixing-model calculations: **Model A** (δ^{13}C of the aboveground biomass), **Model B** (δ^{13}C of the belowground biomass), **Model M** (the calculated δ^{13}C of a 1:1 mixed contribution of aboveground and belowground biomass). (-) indicates that factor dropped out of the ANCOVA model, ns. = not significant.

	Model A		Model B		Model M	
Factors	*F value*	*p value*	*F value*	*p value*	*F value*	*p value*
Site	0.28	ns.	1.07	ns.	2.93	<0.10
Treatment	9.41	**<0.01**	1.58	ns.	2.82	0.10
Distance to marsh edge	0.01	ns.	0.03	ns.	0.08	ns.
Distance to creek	5.12	**<0.05**	0.46	ns.	2.93	<0.10
Relative elevation		-	3.07	<0.10	4.14	<**0.05**
Site x treatment		-		-		-
Site x dist. marsh edge		-	3.51	<0.10		-
Site x dist. creek	9.21	<**0.01**		-	4.27	<**0.05**
Site x rel. elevation		-		-		-
Treat. x dist. marsh edge	5.71	<**0.05**	3.42	<0.10	5.17	<**0.05**
Treat. x dist. creek		-		-		-
Treat. x rel. elevation		-	4.93	**<0.05**		-
Dist. marsh edge x dist. creek		-		-		-
Dist. marsh edge x rel. elevation		-		-		-
Dist. creek x rel. elevation		-		-		-

APPENDIX

Appendix Table A1 Results of ANCOVA analyses testing for effects of single and interacting factors on the δ^{13}C of aboveground plant biomass, belowground plant biomass, and mixed biomass (1:1 aboveground : belowground), referring to the three end-member assumptions used in mixing-model calculations. (-) indicates that factor dropped out of the ANCOVA model, ns. = not significant.

	δ^{13}C aboveground		δ^{13}C belowground		δ^{13}C mixed	
Factors	*F value*	*p value*	*F value*	*p value*	*F value*	*p value*
Site	11.42	**<0.01**	6.45	<**0.05**	16.03	**<0.001**
Treatment		**-**	17.76	**<0.001**	12.07	**<0.01**
Distance to marsh edge		-	0.22	ns.	2.57	ns.
Distance to creek		**-**		-		-
Relative elevation	1.65	ns.		-		-
Site x treatment		-		-		-
Site x dist. marsh edge		-	6.12	**<0.05**		-
Site x dist. creek		-		-		-
Site x rel. elevation	3.86	<0.10		-	3.39	<0.10
Treat. x dist. marsh edge		-		-		-
Treat. x dist. creek		-		-		-
Treat. x rel. elevation		-		**-**		-
Dist. marsh edge x dist. creek		-		-		-
Dist. marsh edge x rel. elevation		-		-		-
Dist. creek x rel. elevation		-		-		-