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Minerogenic salt marshes can function as important inorganic carbon stores

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Abstract

Stocks and fluxes of soil inorganic carbon have long been ignored in the context of coastal carbon sequestration, and their implications for the climate cooling effect of blue carbon ecosystems are complex. Here, we investigate the role of soil inorganic carbon in five salt marshes along the northern coast of the European Wadden Sea, one of the world's largest intertidal areas, harboring ~ 20% of European salt-marsh area. We demonstrate a substantial contribution of inorganic carbon (average: 29%; range: 7–57%) to the total soil carbon stock of the top 1 m. Notably, inorganic exceeded organic carbon stocks in one of the studied sites; a finding that we ascribe to site geomorphic features, such as proximity to marine calcium carbonate sources and hydrodynamic exposure. Contrary to our hypothesis that inorganic carbon stocks would decline along the successional gradient from tidal flat to high marsh, as carbonate deposits would progressively dissolve in increasingly organic-rich rooted sediments, our findings demonstrate the opposite pattern—an increase in inorganic carbon stocks along the successional gradient. This suggests that the dissolution of calcium carbonates in the root zone is counterbalanced by other processes, such as trapping of sedimentary carbonates by marsh vegetation and calcium carbonate precipitation in anaerobic subsoils. In the context of blue carbon, it will be critical to develop an improved understanding of these plant- and microbiota-mediated processes in calcium carbonate cycling.

Blue carbon refers to the organic carbon cycled in vegetated coastal ecosystems, that is, tidal marshes, mangroves, and seagrass meadows, which comprise the most effective long-term carbon sinks of the biosphere. Despite their small areal coverage of ~ 1% of the global ocean surface, blue carbon ecosystems exert an extraordinary leverage over the global carbon cycle by accounting for ~ 50% of the total marine soil (sediment) organic carbon budget (Duarte et al. 2013; Spivak et al. 2019). This role has stimulated great interest in their management as greenhouse gas offsets in carbon-crediting programs (Herr et al. 2017; Needelman et al. 2018). Carbon sequestration in these ecosystems is driven by the interplay of high rates of plant primary production, vertical soil development with rising sea levels, and slow rates of decomposition in reducing soils (Mcleod et al. 2011).

In recent years, a rapidly increasing number of studies refined our insight into soil organic carbon stocks and dynamics of tidal marshes, mangroves, and seagrass beds (Macreadie et al. 2019; Rogers et al. 2019; Ren et al. 2022). By comparison, the stocks and fluxes of inorganic carbon have been largely ignored in the context of coastal carbon sequestration, and their implications for the climate cooling effect of these ecosystems remain unclear (Macreadie et al. 2017; Van Dam et al. 2021). The major part of soil inorganic carbon in blue carbon ecosystems derives from the formation of calcium carbonate ($CaCO_3$), that is, the process of calcification (Saderne et al. 2019), but also dolomite ($CaMg[CO_3]_2$) dynamics could be relevant in some coastal regions (Gunatilaka 1991). Counterintuitively, calcification generates a net flux of CO_2 to the

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Additional Supporting Information may be found in the online version of this article.

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atmosphere, because for each mole of carbon fixed as calcium carbonate, two moles of total alkalinity are consumed, leading to a net increase in water-column pCO_2 (Macreadie et al. 2017). Conversely, the dissolution of calcium carbonates results in a net decrease of pCO_2. In many cases, blue carbon ecosystems primarily act as depositional environments for allochthonous carbonates, which yields the potential for post-depositional dissolution (Macreadie et al. 2017). However, reports are almost restricted to seagrasses and mangroves, given the focus on inorganic carbon dynamics in tropical ecosystems, and there is a surprising lack of data on soil inorganic carbon stocks for tidal marshes. It is generally believed that inorganic carbon represents an unimportant contribution to tidal-marsh total carbon stocks, because rates of in situ calcification are usually negligible, and deposited calcium carbonate from allochthonous sources is assumed to rapidly dissolve under acidifying conditions of the marsh rhizosphere (Saderne et al. 2019).

The salt marshes of the Wadden Sea represent 20% of the European tidal-marsh area (Doody 2008). These marshes are minerogenic ecosystems, characterized by high rates of mineral sediment deposition, resulting in vertical surface accretion frequently exceeding 5 mm yr^{-1} (Esselink et al. 2017). Previous work demonstrated that a large fraction of soil organic carbon preserved in these marshes is of sedimentary, allochthonous origin, which contributes $\sim 25\%$ in the surface soil layer (0–5 cm) and $\sim 70\%$ in the subsoil below 30 cm depth (Mueller et al. 2019*a*,*b*). Given the large fraction of allochthonous soil organic carbon, it is therefore possible that also sedimentary inorganic carbon imports play an important but so far overlooked role in the carbon budget of these ecosystems.

Here, we investigated soil inorganic carbon stocks along the successional gradient from tidal flat (via pioneer zone and low marsh) to high marsh in two geomorphically contrasting tidal flat-salt marsh ecotones of the Wadden Sea: a foreland site and a back-barrier site. Foreland marshes in the Wadden Sea expand seaward from the main seawall and make up the largest share of the Wadden Sea marsh area. Foreland marshes are hydrodynamically exposed systems that experience high amounts of sediment input, particularly, during storm events in fall and winter. Back-barrier marshes are hydrodynamically more sheltered, as they develop in the lee of a barrier or dune system (Esselink et al. 2017). We first hypothesized that soil inorganic carbon stocks are greater at the foreland than at the back-barrier site, because sedimentary carbonate deposition would increase with hydrodynamic exposure and exchange with the marine system. We hypothesized second that soil inorganic carbon stocks would sharply decline along the successional gradient from tidal flat to high marsh, because carbonate deposits would progressively dissolve in increasingly rooted sediments. Finally, we investigated the soil inorganic carbon stocks of three additional high-marsh sites along the northern Wadden Sea coast in order to provide the first comprehensive estimate of soil inorganic carbon stocks for the region (Fig. 1).

Materials and methods

Study sites and sampling: Coastal ecotones

The study was conducted along two geomorphically distinct tidal flat-salt marsh ecotones of the European Wadden Sea—the Skallingen site, Denmark, (a back-barrier site) and the Hamburger Hallig site (a foreland site), Germany (Fig. 1). At both sites, sampling was conducted along four zones of the successional gradient from tidal flat to high marsh (Fig. 2). In minerogenic salt marshes of the Wadden Sea, successional stages are typically reflected in a clear zonation of the plant community composition along an elevation gradient from tidal flat to high marsh (Castillo et al. 2021). In the Wadden Sea, the tidal flat is initially colonized by pioneer plant species, such as *Salicornia* sp. and *Spartina anglica*. Pioneer species are replaced by species from mid- and late-successional stages in the low and high marsh, such as *Puccinellia maritima* and *Elymus athericus* (Rupprecht et al. 2015). The pace of this process depends on the combination of drainage conditions and sedimentation rates in relation to flooding frequency (Leendertse et al. 1997; Olff et al. 1997).

The back-barrier marsh at Skallingen has a tidal amplitude of 1.3 m, with floodwater salinity ranging between 25 and 30 ppt. The brackish high marsh receives freshwater inputs from upland groundwater discharge and is dominated by *Phragmites australis*. The low marsh and pioneer zone are dominated by *Atriplex portulacoides* and *Sp. anglica*, respectively. Soil pH (measured in $CaCl_2$) at the site ranges from 6.5 in the high marsh to 7.8 in the tidal flat (Supporting Information Fig. S1). The foreland salt marsh at Hamburger Hallig (Nolte et al. 2013; Stock 2011) developed adjacent to an old island remnant 3 km off the coast after the construction of a dam connecting island and mainland in 1875. Marshes at Hamburger Hallig experience a tidal range of 3.4 m, with floodwater salinity ranging from 25 to 29 ppt. The vegetation shows a zonation typical for Wadden Sea salt marshes: *Sp. anglica* is dominant in the pioneer zone, *A. portulacoides* and *Pu. maritima* are dominant in the low marsh, and *E. athericus* is dominant in the high marsh (Esselink et al. 2017; Mueller et al. 2020). Soil pH (measured in $CaCl_2$) at the site ranges from 7.2 in the low marsh to 7.5 in the tidal flat (Supporting Information Fig. S1).

Three 100-cm soil cores were sampled from each of the four zones per site ($N = 24$). We used an *Eijkelkamp* peat sampler with a 50-cm long, 500-cm^3 sample head, commonly referred to as Russian peat corer. As the peat sampler cuts sidewise into the soil profile, the technique allowed for uncompacted and undisturbed sampling (Jowsey 1966). The use of the peat sampler for the mineral soils of our sites required precoring with a narrow (4-cm diameter) gouge auger to reduce friction

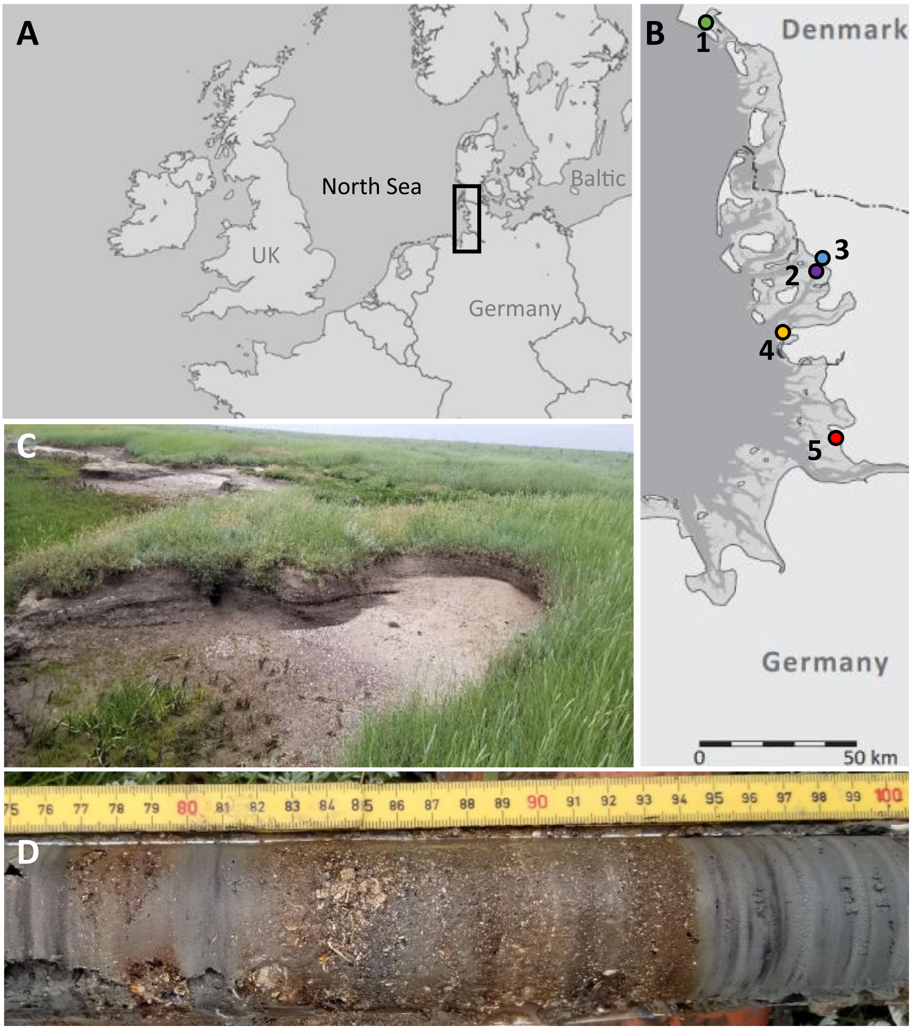

Fig. 1. (**A**,**B**) Study sites along the Wadden Sea coast: (1) Skallingen, (2) Hamburger Hallig, (3) Sönke-Nissen-Koog, (4) Westerhever, (5) Dieksanderkoog. Color-code in (**B**) refers to Fig. 3. (**C**) Marsh-edge cliffs at the Hamburger Hallig foreland site: large amounts of calcareous shell fragments accumulate in pockets along the marsh cliff and get overgrown by secondary pioneer vegetation (*Salicornia* sp., *Spartina* sp.). (**D**) Layers of high shell density in 75–95 cm depth of a soil core sampled in the low marsh at Hamburger Hallig. Photos: T. J. Mozdzer.

resistance during coring. One of the three 100-cm soil cores per successional zone ($n = 4$ per site) was sectioned into ten 10-cm increments. From the other two cores per zone, the following four depth increments were sampled: 0–10, 20–30, 60–70, 90–100 cm.

Regional assessment: Additional high-marsh sites

To evaluate how inorganic carbon accumulation at our two sites compare to other marshes of the Wadden Sea region, we analyzed the soil inorganic carbon density of three additional sites along the 250-km coastline from Skallingen (DK) to the Elbe estuary (DE) (Fig. 1). This assessment was restricted to the mature high-marsh zone of the ecotones not encompassing the inorganic carbon stock development along the entire successional gradient. The three additional sites have previously been sampled to quantify soil organic carbon stocks and organic carbon-sequestration rates (Mueller et al. 2019*b*). For the present study, we used the unpublished data on soil inorganic carbon contents and stocks from the same assessment. Site and sampling details are given in Mueller et al. (2019*b*). Also compare Fig. 1.

Laboratory analyses

Soil samples were dried at 105°C for at least 72 h and weighed to determine bulk density (sample dry weight divided by sample volume). Organic and inorganic carbon contents (% dry weight) of samples from the back-barrier and foreland ecotones were quantified by determining the total carbon content of acid-treated and untreated subsamples using elemental analyzers. Element analysis was coupled to isotope analysis to determine carbon stable-isotope ratios. We used a Costech ECS4010 elemental analyzer coupled to a Picarro G2121-i

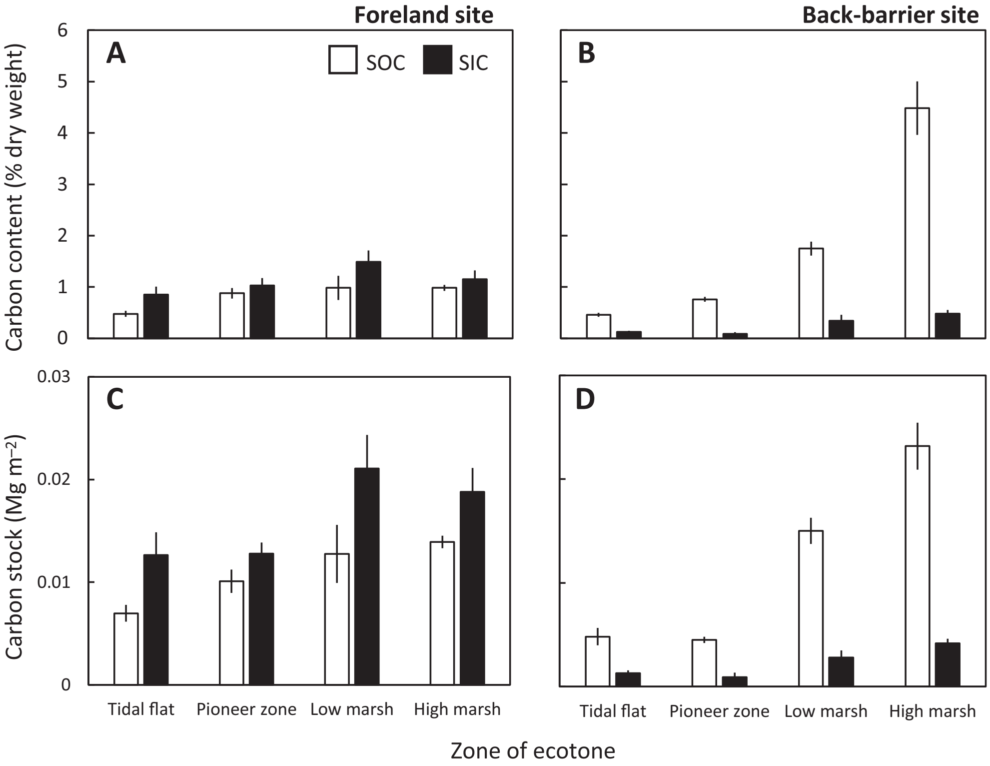

Fig. 2. Soil organic carbon (SOC) and soil inorganic carbon (SIC) contents and stocks of the top 1-m soil (sediment) layer along four successional zones of two tidal flat-salt marsh ecotones in the European Wadden Sea, the foreland site at Hamburger Hallig (**A**,**C**) and the back-barrier site at Skallingen (**B**,**D**). Shown are mean values ± standard error of $n = 3$ cores per successional zone.

isotope analyzer at Bryn Mawr College or an Eurovector EURO-EA 3000 elemental analyzer coupled to a Nu Instruments Nu Horizon isotope ratio mass spectrometer at Hamburg University. Approximately 100–300 mg of subsample was acidified in 1-mL glass vials using 0.1–0.4 mL (depending on reaction strength) of 10% HCl. Acidified subsamples were vented for 12 h at room temperature under a fume hood and subsequently dried at 105°C to constant weight. The carbon content of acid-treated subsamples, accounting for changes in sample mass caused by HCl addition, was considered as organic carbon content. Inorganic carbon contents were calculated subtracting organic carbon contents from total carbon contents of untreated subsamples. Mud vs. sand content was approximated by passing samples through a 0.05-mm test sieve. Grain-size analysis was conducted on all cores sampled at the 10-cm depth resolution ($n = 1$ core/zone).

Data analysis

Data were analyzed using Statistica (TIBCO Software Inc.) and Excel 2016 (Microsoft Corporation). Calculated inorganic carbon contents (i.e., the difference in carbon content between acidified and un-acidified subsamples) < 0% were considered as 0% soil inorganic carbon. Before using calculated inorganic carbon contents > 0% in further statistical analyses, we checked for ^{13}C depletion in acidified vs. un-acidified samples. Inorganic carbon contents of samples that did not show ^{13}C depletion upon acidification were likewise considered as 0% soil inorganic carbon. This data-quality check was conducted to avoid overestimation of inorganic carbon contents and stocks. Soil inorganic and organic carbon stock or density (= carbon mass/soil volume) was calculated by multiplying sample bulk density (= soil dry mass/soil volume) with inorganic and organic carbon contents (mass %), respectively. Carbon-stock and carbon-content data for the entire 100-cm soil profile were calculated by linear interpolation between the four depth sections (i.e., 0–10, 20–30, 60–70, and 90–100 cm) for the soil cores that were only sampled at those four discrete depths. The validity of this assessment was verified by comparing mean soil inorganic carbon contents of the top 100-cm soil layer based on values from linear interpolation with values from higher resolution sampling (i.e., 10 cm increments) in $n = 8$ cores. A paired t-test did not indicate significant differences between interpolated and higher-resolution data ($p = 0.86$). Two-way ANOVA was used to test if organic and inorganic carbon stocks differ between sites (back-barrier vs. foreland; Hypothesis 1) and successional zone (tidal flat vs. pioneer zone vs. low marsh vs. high marsh; Hypothesis 2). Prior ANOVA testing, we visually checked for normal distribution of residuals and homogeneity of variances across groups. Due to the fully balanced study design, potential moderate

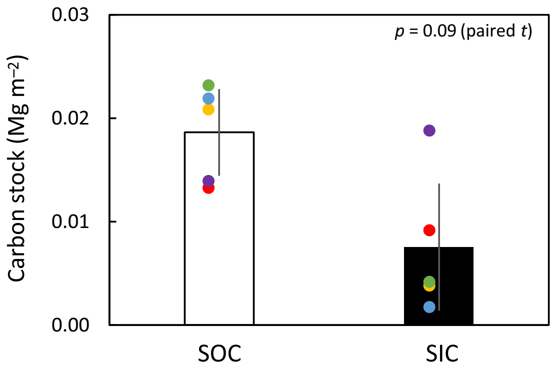

Fig. 3. Comparison of soil organic (SOC) vs. inorganic carbon (SIC) stocks of the top 1-m soil layer of $n = 5$ mature (i.e., high marsh) sites along the Wadden Sea coastline between Skallingen (DK) and the Elbe estuary (DE). Shown are mean values ± standard deviation. Single data points, color-coded by site, are overlaid. Site locations are depicted in Fig. 1B.

deviations from homogeneity of variance between groups were considered unimportant for ANOVA testing (Box 1954; McGuinness 2002). A paired *t*-test was used to compare organic with inorganic carbon stocks of the five high-marsh sites. We tested for relationships between mud/sand contents and carbon contents using linear and nonlinear ordinary least-squares regression.

Results

Soil inorganic vs. organic carbon stocks across sites and successional zones

Soil inorganic carbon contents and stocks of the top 1 m were significantly greater at the foreland site than at the back-barrier site (Fig. 2; Table 1). Inorganic contents and stocks increased along the successional gradient from tidal flat to low and high marsh (Fig. 2). The effect of zone was significant based on two-way ANOVA (Table 1).

Soil inorganic carbon stocks were significantly greater than soil organic carbon stocks at the foreland site (paired *t*-test: $p < 0.01$), whereas the opposite was true for the back-barrier site ($p < 0.001$; Fig. 2).

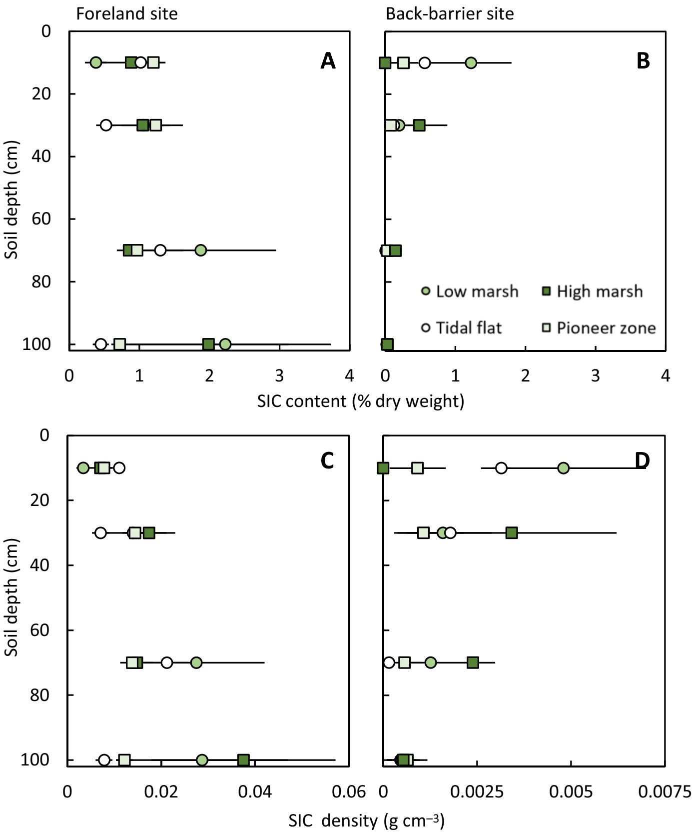

Fig. 4. Soil inorganic carbon content and density in relation to soil depth and successional zone of two tidal flat-salt marsh ecotones in the European Wadden Sea, the foreland site at Hamburger Hallig (**A**,**C**) and the back-barrier site at Skallingen (**B**,**D**). Shown are mean values ± standard error ($n = 3$).

Soil organic carbon contents and stocks of the top 1 m showed a clearer increase along the successional gradient than inorganic carbon contents and stocks (Fig. 2; Table 1). Site effects on soil organic carbon differed markedly from the inorganic carbon results. While organic carbon contents were significantly greater at the back-barrier than foreland site, there was no difference in organic carbon stocks between sites (Fig. 2; Table 1).

Expanding the comparison of soil inorganic vs. organic carbon stocks to a larger number of high-marsh sites along the northern Wadden Sea coast (Fig. 1B) revealed that

Table 1. Output of two-way ANOVA tests for the effects of site and successional zone on soil organic carbon (SOC) and soil inorganic carbon (SIC) contents and stocks of the top 1-m soil (sediment) layer at the two sites, Hamburger Hallig (foreland site) and Skallingen (back-barrier site).

	SOC content		SIC content		SOC stock		SIC stock	
ANOVA	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*
Site	**<0.001**	31.85	**<0.001**	56.28	0.475	0.54	**<0.001**	91.23
Zone	**<0.001**	29.67	**0.058**	3.07	**<0.001**	20.84	**0.039**	3.54
Site * zone	**<0.001**	21.31	**0.072**	0.90	**0.006**	6.15	0.354	1.17

Note: Values are highlighted in bold at $p \leq 0.1$.

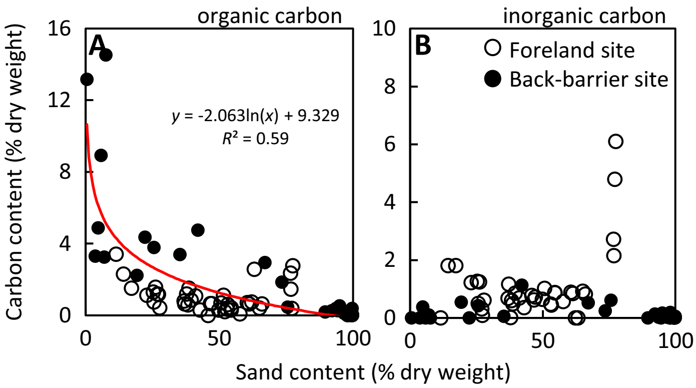

Fig. 5. Soil organic (**A**) and inorganic (**B**) carbon content as a function of sand content. Depicted are data from eight 1-m soil cores (one per successional zone and site) sectioned into ten 10-cm increments ($N = 80$).

greater inorganic vs. organic carbon stocks represent an exception (Fig. 3). Overall, mean soil organic carbon stocks of the top 1 m were > 100% greater than inorganic carbon stocks; although this difference was only marginally significant due to high variability in inorganic carbon stocks across sites (Fig. 3).

Soil inorganic carbon in relation to soil depth and grain size

Observed increases in soil inorganic carbon stocks of the top 1 m from tidal flat to high marsh (Fig. 2) were largely driven by differences in inorganic carbon below 20 cm soil depth (Fig. 4). Inorganic carbon densities of the topsoil (0–10 cm) showed the opposite relationship with greater inorganic carbon values in tidal flat vs. high marsh in both sites (Fig. 4C,D).

The soil-depth distribution of soil inorganic carbon differed markedly between the foreland and back-barrier site. Specifically, inorganic carbon contents of the low and high marsh showed an increasing trend with soil depth at the foreland site but generally decreased at the back-barrier site (Fig. 4).

Sand content was an important predictor of soil organic carbon content and density across depths and sites, explaining approximately 59% of organic carbon-content variability (Fig. 5A). In contrast, no relationship was observed between inorganic carbon content and grain-size distribution (Fig. 5B).

Discussion

Soil inorganic carbon stocks of Wadden Sea salt marshes

The present survey including five salt-marsh sites along the northern Wadden Sea coast reveals a soil inorganic carbon stock for the top 1 m of soil of 75 Mg ha^{-1} (range: 17–188), which represents a substantial contribution of inorganic carbon to the total soil carbon stock of these ecosystems (29%; range: 7–57%). Notably, one of the sites supported even greater soil inorganic than organic carbon stocks (Fig. 3). Our observed inorganic carbon densities, median = 4 mg cm^{-3} (IQR = 5 mg cm^{-3}), are comparable to global median (and IQR) values reported for mangroves of 1 (21) mg cm^{-3} but are lower than those reported for seagrass beds, 59 (66) mg cm^{-3}, as reported in the first meta-analysis on carbonate dynamics in blue carbon ecosystems (Saderne et al. 2019). There are few studies reporting soil inorganic carbon contents for tidal-marsh ecosystems (Vranken et al. 1990; Zwolsman et al. 1993; Spohn et al. 2013; Saderne et al. 2019), and even fewer providing soil inorganic carbon stock (or density) data for tidal marshes that could be used to compare our findings with. Specifically, Saderne et al. (2018) reported extreme mean soil inorganic carbon stocks of 970 Mg ha^{-1} for marsh-related *sabkha* ecosystems of the Arabian Peninsula, and Zhang et al. (2021) report mean soil inorganic carbon stocks of ~ 150 Mg ha^{-1} for a minerogenic estuarine salt marsh on the Yellow River Delta, a finding that falls well within the range reported here.

Our findings of large inorganic carbon stocks challenge the prevailing notion that tidal marshes are unimportant inorganic carbon stores compared to other blue carbon ecosystems, that is, mangroves and seagrass beds (Saderne et al. 2019). Tidal marshes have an exceptionally high potential for calcium carbonate dissolution in soils (Vranken et al. 1990) and a relatively low abundance of calcifying organisms (Saderne et al. 2019). We do not have any data to suggest the opposite for the salt marshes of the Wadden Sea. Instead, we argue that calcium carbonate accumulation represents an inherently large, but overlooked feature of many minerogenic tidal-marsh ecosystems. Vertical soil development in minerogenic marshes is primarily driven by high rates of mineral sediment deposition (Allen 2000); and thus, calcium carbonate inputs can be substantial, depending on site geomorphology, proximity of marine or riverine carbonate sources, and the carbonate concentration of suspended sediments (Allen 1987; Larsonneur 1994).

Inorganic vs. organic carbon stock development

Our data suggest that geomorphic setting acts an important predictor of marsh soil inorganic carbon stocks, as it controls the frequency and amount of carbonate deposition. Specifically, we found soil inorganic carbon stocks were much greater in the foreland ecotone at Hamburger Hallig than in the back-barrier ecotone at Skallingen, which supports our first hypothesis that inorganic carbon accumulation is more pronounced at hydrodynamically exposed sites, with high marine exchange, than at sites that are hydrodynamically more sheltered with lower marine exchange (Fig. 2). Greater marine exchange at the foreland than back-barrier site is further supported by the δ^{13}C signature of organic carbon accumulating in the surface soil of the high marsh (Supporting Information Fig. S1). These ^{13}C-enriched signatures at the foreland site indicate a larger relative contribution of marine-derived organic carbon to the total organic carbon pool (Mueller et al. 2020).

In contrast to the inorganic carbon results, soil organic carbon stocks did not significantly differ between sites (Fig. 2; Table 1). This finding is in accordance with previous work in the region demonstrating relatively constrained soil organic carbon densities for whole-soil profiles (i.e., ≥ 100 cm depth) across Wadden Sea salt marshes, independent of site geomorphology (Mueller et al. 2019*b*). Despite similar average site-level organic carbon stocks, the two sites showed markedly different organic-carbon trends along the successional gradient from tidal flat to high marsh (Table 1). Specifically, tidal-flat and pioneer-zone organic carbon stocks tended to be lower at the back-barrier than the foreland site; whereas the opposite is true for the low and high marsh (Fig. 2). We argue that this pattern is caused by a more extreme distribution of sand contents at the back-barrier site ranging from > 99% sand in some sediment layers of the tidal flat to < 1% sand in the high marsh. Sand content at the foreland site show far less variability across soil depths and zones and consequently less variability in organic carbon contents and stocks (Fig. 5). We argue that this distribution results from the greater hydrodynamic exposition of the foreland site, allowing for greater deposition of large grains at high elevations (Allen 1992, 2000; Müller-Navarra et al. 2016).

Our data demonstrate an unexpected increase in inorganic carbon stocks along the successional gradient with stocks maximized in the low or high marsh. These patterns of inorganic carbon stocks along successional gradients were relatively consistent between sites (Table 1; Fig. 2). We originally hypothesized inorganic carbon stocks to decline along this gradient as calcium carbonate deposits would progressively dissolve in increasingly rooted sediments. Although our findings do not exclude an increase in carbonate dissolution rates along the successional gradient, they do suggest that any potential increase in carbonate dissolution gets overcompensated by other plant-mediated and microbially mediated processes, such as trapping of sedimentary carbonates by marsh vegetation and calcium carbonate precipitation in anaerobic subsoils.

It is well established that plants effectively trap sediment from the water column and thereby increase mineral sediment deposition compared to unvegetated areas (Morris et al. 2002; Kirwan and Megonigal 2013). Therefore, plant-mediated carbonate deposition likely contributed to greater inorganic carbon stocks in marsh vs. tidal-flat soils (Fig. 6). Precipitation of calcium carbonates below the acidifying conditions of the rhizosphere could act as an additional driver of high inorganic carbon stocks in marsh soils in relation to the tidal flat (Vranken et al. 1990). This process can be mediated by the production of bicarbonate ions and the consumption of protons by anaerobic microbial communities. For instance, Rassmann et al. (2016) demonstrated a strong association of calcium carbonate precipitation with anaerobic microbial metabolism in the sediments of the Rhône delta. Anaerobic metabolism, and thus carbonate precipitation, increased with sediment organic matter contents and decreasing distance to the delta. Similarly, increasing organic matter availability along the gradient from tidal flat to high marsh could support greater rates of anaerobic microbial metabolism and coupled carbonate precipitation in the present study. In support of this notion, the observed increase in soil inorganic carbon stocks

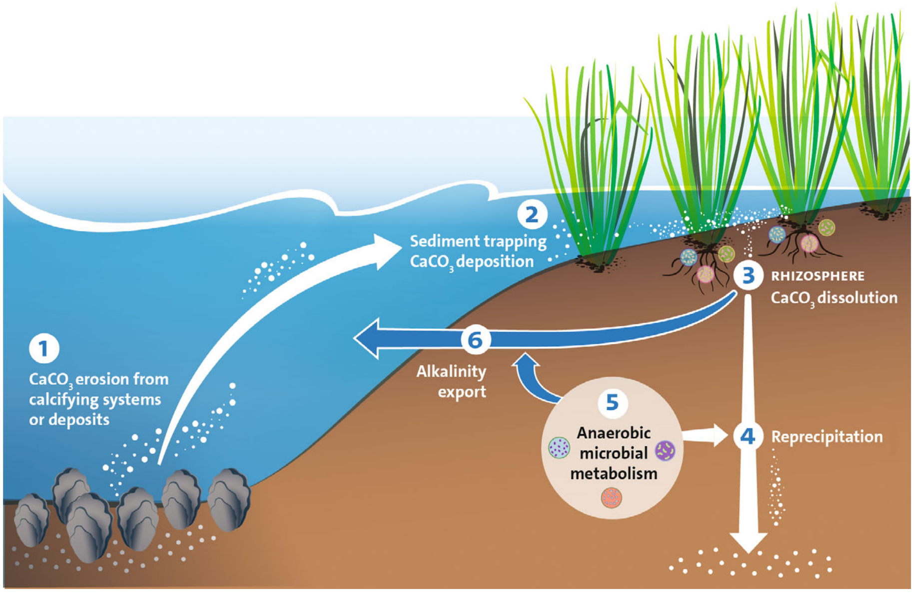

Fig. 6. Conceptual diagram illustrating the potential contribution of allochthonous calcium carbonate input and dissolution to the alkalinity export from tidal marshes. Our quantitative insight into the processes (1–6) shown here is yet scarce or absent, but will be critical to develop a mechanistic understanding of coastal carbonate dynamics and their leverage over marsh CO_2 and alkalinity budgets. Image by courtesy of UHH/Wohlfahrt.

of the top 1 m from tidal flat to high marsh (Fig. 2) was driven by differences in inorganic carbon in deep soil layers, where conditions are frequently or permanently anoxic and support anaerobic microbial metabolism (Fig. 4; Tang et al. 2022).

The soil profiles investigated at the foreland site revealed an additional important contributor to larger inorganic carbon stocks in marsh vs. tidal-flat soils. Here, a large fraction of the inorganic carbon stock was found in deeper layers of extremely high inorganic carbon density, largely composed of comminuted shell debris (Figs. 1C,D, 4). These shell deposits could result from storm surges translocating shell fragments from unvegetated intertidal and subtidal environments to the salt marsh, were they get trapped by the vegetation (Allen 1987). Furthermore, we found evidence that shell accumulation might reflect a phase of the early marsh development. Specifically, we observed large amounts of shell debris accumulating in pockets and gullies of the mash-edge cliff, where they are being overgrown by secondary pioneer vegetation (Fig. 1C). The formation of marsh cliffs through edge erosion and regrowth of marsh in front of the cliff are intrinsic processes of natural salt-marsh dynamics (van de Koppel et al. 2005). At the foreland site, marsh cliffs provide an effective deposition environment for large amounts of shell debris. The phenomenon of cliff-fringing shell deposits is not specific to our study site at Hamburger Hallig, or salt marshes of the Wadden Sea region, but has been reported for other coastal environments worldwide, such as the Jiangsu Coast, China (Zhao et al. 2017) and San Francisco Bay, California (Baye et al. 2020). Therefore, it is possible that the cyclical process of marsh-cliff erosion and regrowth could represent an important driver of inorganic carbon accumulation in coastal ecotones that warrants further investigation.

Changes in inorganic carbon content with soil depth should be interpreted cautiously, especially in the context of carbonate dynamics, where the inorganic–carbon change with depth may reflect succession in young marsh ecosystems. Declining inorganic carbon contents with soil depth have previously been interpreted as evidence of postdepositional carbonate dissolution (Vranken et al. 1990; Zhang et al. 2021). In the present study, inorganic–carbon declines with soil depth were only observed at the Skallingen site. Here, decline slopes were indeed steeper in the low and high marsh than in the pioneer zone and tidal flat, potentially indicating greater carbonate dissolution rates in more rooted soils (Fig. 4). However, our study also demonstrated that inorganic carbon stocks can undergo a marked change during succession, so that inorganic–carbon changes with soil depth may likewise reflect the chronosequence of salt-marsh development from tidal flat (Mueller et al. 2019*b*).

Perspective and knowledge gaps

We currently know little about the importance of different pedogenic and biogenic calcium carbonate sources feeding tidal marsh inorganic carbon stocks. The present study provides evidence that the deposition of shell debris, derived from adjacent marine ecosystems, can be one important carbonate input to marsh ecosystems. If this finding applies more widely to other coastal regions, it may yield important implications for CO_2 and alkalinity budgets at the landscape scale of the coastal zone (i.e., the coastal seascape). A growing number of reports suggests that interactions between spatially associated coastal ecosystems via long-distance facilitative processes can enhance the blue carbon potential of the seascape (Huxham et al. 2018; Ren et al. 2022). Similarly, connectivity of coastal ecosystems may also represent an important factor determining calcium carbonate dynamics and thus the alkalinity budget at the seascape scale. That is, calcium carbonate can be translocated or eroded from calcifying ecosystems, such as corals or bivalve reefs, and deposited and dissolved in tidal-marsh ecosystems (Fig. 6). In this way, alkalinity consumption in calcifying ecosystems may be counterbalanced by alkalinity production in ecosystems that support greater rates of carbonate dissolution. The exchange of calcium carbonate between ecosystems within the coastal seascape has yet poorly been explored (Saderne et al. 2019), and new methodological approaches that facilitate tracing carbon fluxes within the coastal seascape will be needed to develop a quantitative understanding of these fluxes.

Plants are likely to control two key processes of the tidal-marsh calcium carbonate balance. First, aboveground plant structures effectively trap sediment from the water column and thus, determine the rate of allochthonous calcium carbonate input to the ecosystem. Second, plant–microbe interactions in the rhizosphere yield a high potential to facilitate or accelerate carbonate dissolution. Plant roots stimulate soil microbial activity by supplying oxygen to an otherwise anoxic soil environment via root oxygen loss and by releasing labile organic substrates via rhizodeposition, thereby exerting primary control over soil organic carbon cycling (Mueller et al. 2016; Spivak et al. 2019; Ren et al. 2022; Bernal et al. 2023). The same plant–microbe interactions can also lead to a strong acidification of the rhizosphere, driven by rising soil CO_2 levels and the reoxidation of reduced metabolites (Ku et al. 1999; Koop-Jakobsen et al. 2018), which likely facilitates or accelerates carbonate dissolution (Burdige and Zimmerman 2002; Fig. 6). However, experimental support for this potentially important link between plant–microbe interactions and calcium carbonate dissolution in coastal ecosystems is yet lacking. New methodological approaches in the field of wetland rhizosphere research are needed to close this important knowledge gap in our understanding of coastal carbonate dynamics. Recent developments in the field of rhizosphere imaging, such as planar optode imaging of rhizosphere O_2, CO_2, and pH dynamics (Koop-Jakobsen et al. 2018, 2021), appear promising to advance our mechanistic and quantitative understanding in this context.

The export dynamics of dissolved inorganic carbon, including alkalinity, from tidal marshes to adjacent estuarine or coastal waters are poorly understood, but yield important implications for coastal ocean acidification and atmosphere–water CO_2 exchange. The few studies that assessed alkalinity export from tidal marshes only considered anaerobic microbial respiration in soils (i.e., sulfate reduction, denitrification) as a source of alkalinity (Sippo et al. 2016; Wang et al. 2016; Maher et al. 2018). The potentially important role of sedimentary carbonate dissolution in marsh soils as a source of alkalinity to coastal waters has never been investigated, probably because past studies have been conducted in sediment poor, organogenic ecosystems with negligible calcium carbonate inputs. This represents a critical knowledge gap in our mechanistic understanding of coastal dissolved inorganic carbon dynamics and their potential leverage over the CO_2 and alkalinity balance of tidal marshes.

Conclusion

Our study demonstrated that inorganic carbon can represent an important fraction of the total soil carbon stock in minerogenic salt marshes, and that these ecosystems can act as important depositional environments for inorganic carbon. This observation highlights the need to develop a deeper mechanistic and quantitative understanding of inorganic carbon fluxes in minerogenic salt marshes as well as between marshes and adjacent marine ecosystems within the coastal seascape (Fig. 6). For the interpretation of soil inorganic carbon in the context of blue carbon and, more specifically, the climate change-mitigation capacity of tidal marshes, it is critical to develop an improved understanding of calcium carbonate fluxes rather than stocks. Overall, we know little about the quantitative importance of different potential pedogenic and biogenic carbonate sources feeding salt marsh inorganic carbon stocks, rates of carbonate dissolution and reprecipitation in soils, and the contribution of carbonate dissolution to alkalinity export from coastal ecosystems (Fig. 6).

Data availability statement

Data are available upon reasonable request.

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Conflict of interest

None declared.

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