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Key Points:
- Seagrass meadows in OC-rich reef sediments show notably higher alkalinity fluxes, enhancing their CO_2 uptake potential
- The restoration of seagrass meadows in high-OC reef sediments could substantially increase their contribution to carbon removal

Supporting Information:

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

Correspondence to:

W.-C. Chou,
wcchou@mail.ntou.edu.tw

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Author Contributions:

Conceptualization: Wen-Chen Chou, Chin-Chang Hung
Data curation: Lan-Feng Fan, Zih-Wei Tang, Huei-Fen Chen, Ping-Chun Chen, En-Cheng Kong, Yung-Yen Shih, Wei-Jen Huang
Formal analysis: Lan-Feng Fan, Mariche B. Natividad
Funding acquisition: Wen-Chen Chou
Investigation: Wen-Chen Chou, Lan-Feng Fan, Zih-Wei Tang, Ping-Chun Chen, En-Cheng Kong, Yung-Yen Shih, Wei-Jen Huang, Chin-Chang Hung
Methodology: Wen-Chen Chou, Jian-Jhih Chen, Huei-Fen Chen

Contrasting CO_2 Dynamics in Seagrass Meadows Between Organic Carbon (OC)-Rich Reef and OC-Poor Terrestrial Sediments: Implications for Enhanced Alkalinity Production

Wen-Chen Chou[1,2,3], Lan-Feng Fan[1], Mariche B. Natividad[1,4,5], Jian-Jhih Chen[6,7], Zih-Wei Tang[8], Huei-Fen Chen[8], Ping-Chun Chen[1], En-Cheng Kong[1], Yung-Yen Shih[7,9], Wei-Jen Huang[7], and Chin-Chang Hung[7]

[1]Institute of Marine Environment and Ecology, National Taiwan Ocean University, Keelung, Taiwan, [2]Center of Excellence for the Oceans, National Taiwan Ocean University, Keelung, Taiwan, [3]Institute of Marine Biology, National Dong Hwa University, Pingtung, Taiwan, [4]Doctoral Degree Program on Ocean Resources and Environmental Changes, National Taiwan Ocean University, Keelung, Taiwan, [5]Ecosystems Research and Development Bureau, Laguna, Philippines, [6]Department of Marine Environmental Engineering, National Kaohsiung University of Science and Technology, Kaohsiung, Taiwan, [7]Department of Oceanography, National Sun Yat-sen University, Kaohsiung, Taiwan, [8]Institute of Earth Sciences, National Taiwan Ocean University, Keelung, Taiwan, [9]Department of Applied Science, R.O.C. Naval Academy, Kaohsiung, Taiwan

Abstract Seagrass meadows are increasingly recognized across the globe as a natural climate solution due to their significant potential in alkalinity-driven carbon dioxide (CO_2) removal, which possibly represents an overlooked component of ocean carbon removal. This study comprehensively investigated the carbonate chemistry, sediment carbon content, mineral composition, and benthic alkalinity fluxes in two distinct sites with tropical seagrass meadows: one situated in organic carbon (OC)-rich reef sediments and the other in OC-poor terrestrial sediments. Results showed nearly two orders of magnitude higher benthic alkalinity fluxes in the OC-rich reefs than in OC-poor sediments (72.8 ± 64.4 vs. 0.53 ± 0.99 mmol m^{-2} d^{-1}). This can further substantially increase alkalinity levels and reduce the partial pressure of CO_2 in the overlying seawater, thereby enhancing the capacity for CO_2 uptake. We propose that seagrass meadows on high-OC reef sediments, the hotspots for alkalinity generation, could amplify the climate change mitigation potential of seagrass restoration initiatives.

Plain Language Summary Seagrass meadows, renowned for their high productivity, play a crucial role in carbon dioxide (CO_2) removal through photosynthesis, presenting a valuable nature-based climate change mitigation and adaptation strategy. Recent investigations highlight an underappreciated facet of blue carbon dynamics: a significant contribution of sedimentary alkalinity production. Our current study reveals that seagrass meadows growing in reef sediments with elevated organic carbon (OC) content exhibit two orders of magnitude greater sedimentary alkalinity flux than in meadows with lower OC content. Remarkably, these meadows demonstrate a significantly lower partial pressure of CO_2 in the overlying water compared to counterparts in terrestrial sediments with lower OC content. This finding suggests seagrass meadows on high-OC reef sediments as potent hotspots for ocean alkalinity production. Consequently, prioritizing the restoration of seagrasses in such environments might substantially amplify the climate change mitigation potential of seagrass restoration initiatives.

1. Introduction

Coastal blue carbon ecosystems (CBCEs), including mangroves, seagrasses, and salt marshes, are highly productive. They convert atmospheric CO_2 to organic biomass efficiently and bury carbon in sediments. Coastal blue carbon ecosystems (CBCEs) have a high carbon burial rate per unit area and have been acknowledged as a promising ocean-based carbon dioxide removal (CDR) approach, with several valuable co-benefits such as sustaining rich biodiversity, providing flood and storm protection, and mitigating ocean acidification (Macreadie et al., 2021; Nellemann et al., 2009). While the focus has been on the production of organic carbon (OC) through photosynthesis, recent studies show that sedimentary total alkalinity (TA), linked to increased rates of anaerobic respiration and calcium carbonate ($CaCO_3$) dissolution within sediments, may represent an overlooked component of CBCEs (Chen et al., 2024; Fakhraee et al., 2023; Reithmaier et al., 2023; Saderne et al., 2021).

Project administration: Wen-Chen Chou, Lan-Feng Fan
Resources: Lan-Feng Fan, Chin-Chang Hung
Software: Lan-Feng Fan, Mariche B. Natividad
Supervision: Wen-Chen Chou
Validation: Wen-Chen Chou, Lan-Feng Fan, Mariche B. Natividad, Jian-Jhih Chen, Yung-Yen Shih, Wei-Jen Huang, Chin-Chang Hung
Visualization: Lan-Feng Fan, Mariche B. Natividad
Writing – original draft: Wen-Chen Chou, Lan-Feng Fan, Mariche B. Natividad, Jian-Jhih Chen, Zih-Wei Tang, Huei-Fen Chen, Yung-Yen Shih, Wei-Jen Huang
Writing – review & editing: Wen-Chen Chou, Jian-Jhih Chen

Alkalinity generation is strongly associated with OC degradation, following a diagenetic sequence from aerobic reactions near the surface to anaerobic processes in deep sediments (Santos et al., 2021). Aerobic degradation of OC yields CO_2 through the following reaction:

$$CH_2O + O_2 \rightarrow CO_2 + H_2O \tag{1}$$

This results in a return of CO_2 to the environment, representing net-zero long-term carbon removal. However, in certain tropical and subtropical reef systems, aerobic respiration of OC within CBCEs (e.g., seagrasses/mangroves) can trigger the dissolution of carbonate deposits, through "metabolic carbonate dissolution" (Burdige & Zimmerman, 2002; Chou et al., 2021). Oxygen released by the roots of seagrasses/mangroves enhances sediment aerobic respiration, releasing CO_2 and lowering pH, thereby promoting carbonate sediment dissolution, as represented by the following reaction:

$$CO_2 + H_2O + CaCO_3 \rightarrow Ca^{2+} + 2HCO_3^{-} \tag{2}$$

The net reaction in Equations 1 and 2 generates dissolved inorganic carbon ,DIC and TA in a 1:1 ratio, as illustrated in Equation 3:

$$CH_2O + O_2 + CaCO_3 \rightarrow Ca^{2+} + 2HCO_3^{-} \tag{3}$$

Eventually, the bicarbonate generated by reaction (3) diffuses or advects into the overlying waters. Therefore, seagrasses/mangroves-derived OC can generate TA through this process under aerobic conditions, lowering the partial pressure of CO_2 (pCO_2) and improving CO_2 uptake. When oxygen is depleted, anaerobic respiration of OC proceeds in a sequence of denitrification, manganese reduction, iron reduction, sulfate reduction, and methanogenesis (Burdige, 2011). With the abundance of sulfate in seawater compared to other oxidants, the key anaerobic process emerges to the reduction of sulfate coupled with pyrite (FeS_2) and iron monosulfide (FeS) that converts sediment OC to DIC and TA (Reithmaier et al., 2021):

$$6CH_2O + 3SO_4^{2-} + 2FeOOH \rightarrow FeS + FeS_2 + 6HCO_3^{-} + 4H_2O \tag{4}$$

This reaction results in net production of DIC and TA in a 1:1 ratio. Similar to metabolically mediated $CaCO_3$ dissolution, the bicarbonate generated upon sulfate reduction eventually escapes into the overlying waters, contributing to the uptake of atmospheric CO_2. According to a recent global synthesis, the global average outwelling rates of TA are similar to organic burial rates in saltmarshes and three times higher in mangroves (Reithmaier et al., 2023).

This finding suggests that TA may play a more critical role in CO_2 uptake than OC deposition in CBCEs. However, the contribution of TA to CO_2 uptake in seagrass meadows remains to be fully understood due to varying benthic properties that further complicate carbonate chemistry. To address this gap, we compared the carbonate chemistry of the overlying water and porewater, sediment carbon content, mineral composition, and benthic TA and DIC fluxes between two contrasting seagrass meadows, one located in OC-rich reef sediments and another in OC-poor terrestrial sediments. We found that the former exhibits two orders of magnitude higher sedimentary alkalinity flux than the latter, suggesting that seagrass meadows on OC-rich reef sediments could enhance metabolically induced carbonate dissolution and/or sulfate reduction. Consequently, these meadows may serve as hotspots for TA production, thereby enhancing the CDR capacity of CBCEs.

2. Materials and Methods

2.1. Study Sites

The study was conducted in seagrass meadows of Dongsha Island (DS) and Kenting (KT) (Figure 1). The DS, located in the northern South China Sea (SCS), is a remote reef island and is considered a pristine system. The KT site, located at the southern tip of Taiwan, characterizes several brook discharges and receives a slightly terrestrial influence. Both sites are meadows with multiple seagrass species; DS is dominated by *Thalassia hemprichii* and *Cymodocea rotundata* (Lee et al., 2015), while KT is dominated by *Halodule uninervis* and *Thalassia hemprichii*.

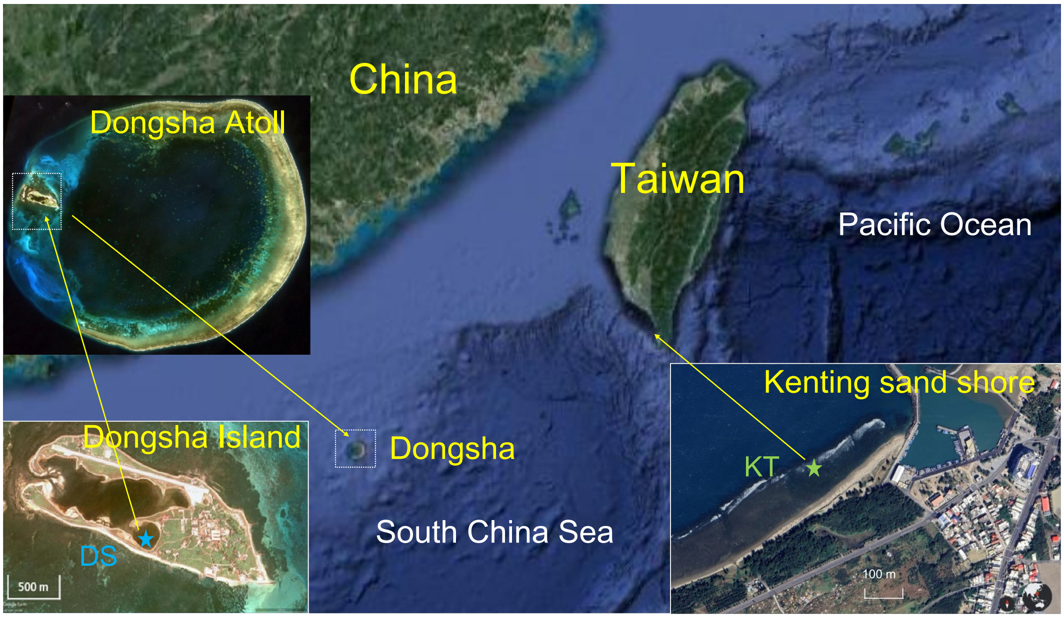

Figure 1. A geographical map indicating the locations of Dongsha Atoll, Dongsha Island (DS, 20°42′04′N, 116°43′24″E), Kenting sand shore (KT, 22°05′14′N, 120°42′20′E), and the selected sampling sites in these regions.

Seagrass coverage at DS slightly exceeds that of KT (85% vs. 75%; Huang et al., 2015). See Text S1, Table S1, and Figures S1 to S3 in Supporting Information S1 for detailed site description.

2.2. Sample Collection and Analyses

The DS site was investigated from January 15–17, 2021, and September 9–11, 2021, for the dry and wet seasons, respectively. The KT site was investigated from May 19–22, 2022, and September 27–2 October 2022 for the wet and dry seasons, correspondingly. Sediment samples were taken once: DS in January 2021 and KT in May 2023.

Discrete seawater samples for TA, DIC, and pH measurements were taken at 06:00, 12:00, and 18:00 daily at DS and 4-hr intervals at KT. Porewater samples were collected using porewater wells and a Luer-Lok syringe from various sediment depths (2, 4, 6, 8, 12, 16, and 20 cm) (Falter & Sansone, 2000). Sediment samples were collected using an acrylic push core (7 cm diameter, 1 m length). Subsamples, collected every 5 cm from top to bottom, were microscopically examined under a Leica WILD M8 microscope and using EOS Utility software. Semi-quantitative analysis of major minerals in surface sediment utilized X-ray powder diffraction with a Bruker D2 Phaser instrument (Chen et al., 2011; Lo et al., 2017).

TA, DIC, and pH were measured following the methods of Dickson et al. (2007), which were consistent with our previous studies (Chou et al., 2018, 2021). The partial pCO_2 and aragonite saturation state (Ω_{Ar}) were calculated from the measured DIC and TA data using the Excel macro CO2SYS version 2.1 (Pelletier et al., 2011). Pore-water calcium ion concentration was determined using an inductively coupled plasma mass spectrometry system (Su & Ho, 2019). Total organic carbon (TOC), total inorganic carbon (TIC), and total nitrogen (TN) in the sediments were determined using an elemental analyzer (Wan, 2023; Yang, 2023). Sample collection, analysis, and instrument procedures are detailed in the Supplemental Methods.

2.3. Benthic Flux Incubations and Calculations

Benthic fluxes were measured with chambers inserted 10–15 cm into the sediment (Roth et al., 2019). Seawater samples from the chambers were taken at 6-hr intervals at DS and 3-hr intervals at KT.

The benthic flux of TA and DIC, denoted as F_{TA}^{SEDI} and F_{DIC}^{SEDI}, respectively, were calculated using the following equation:

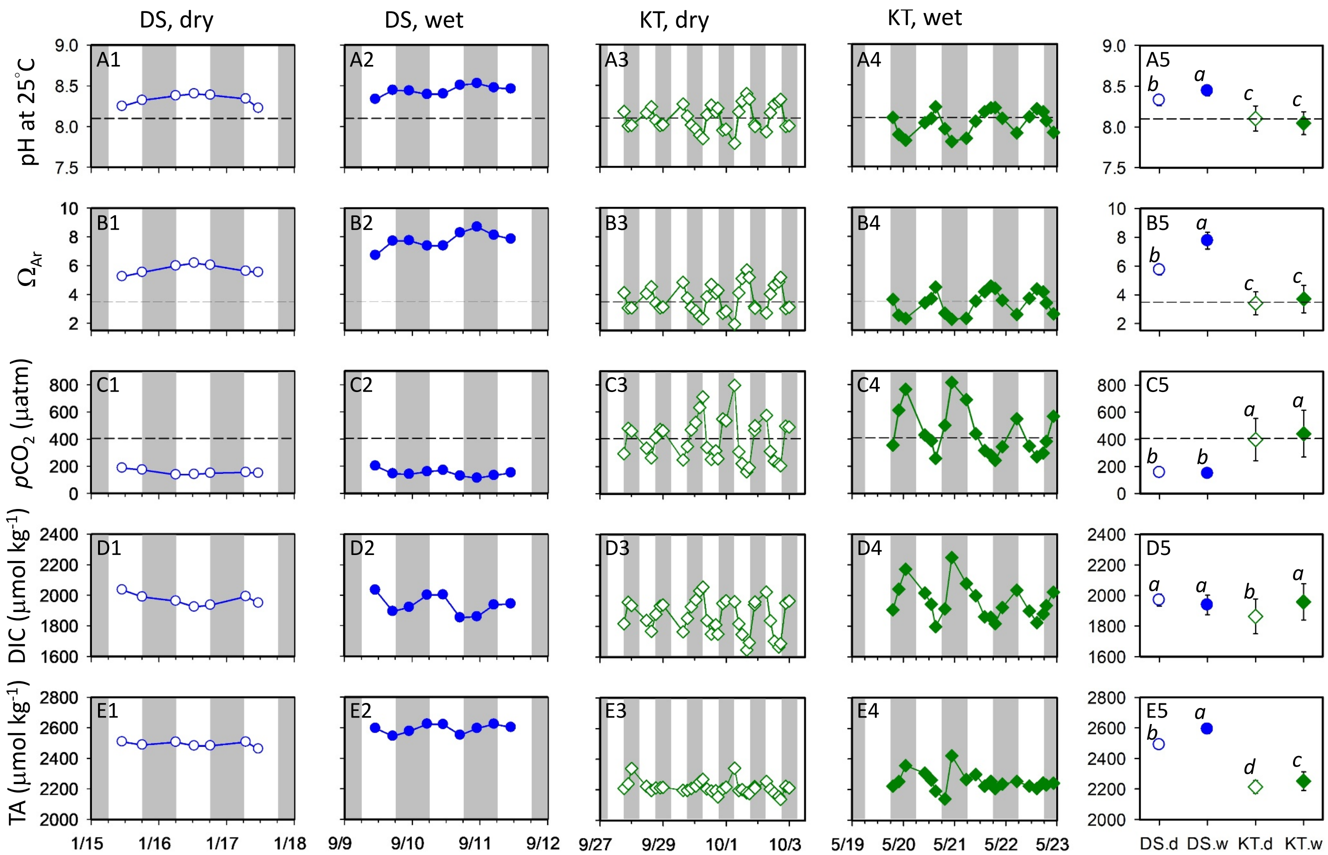

Figure 2. Daily variations in pH (A1–A4), Ω_{Ar} (B1–B4), pressure of CO_2 (pCO_2) (C1–C4), dissolved inorganic carbon (D1–D4), and total alkalinity (E1–E4) in Dongsha islands (DS) and Kenting (KT) during dry and wet seasons. Statistical results are also provided (A5, B5, C5, D5, and E5). Horizontal dashed lines in A, B, and C represent the average open South China Sea (SCS) pH (Tseng et al., 2007), atmospheric pCO_2 (monthly mean at Manua Loa), and open SCS Ω_{Ar} (Tseng et al., 2007) levels, respectively. The disparity in Italicized letters within the panels denotes statistically significant differences based on post-hoc test results ($p < 0.05$) from Wilcoxon's robust Analysis of Variance. DIC, dissolved inorganic carbon; TA, total alkalinity; SCS, South China Sea.

$$F_{\mathrm{TA}}^{\mathrm{SEDI}} = \frac{\Delta \mathrm{TA}}{\Delta t} \times h\rho \tag{5}$$

$$F_{\mathrm{DIC}}^{\mathrm{SEDI}} = \frac{\Delta \mathrm{DIC}}{\Delta t} \times h\rho \tag{6}$$

where ΔTA and ΔDIC represent the differences in TA and DIC, respectively, during the incubation period Δt (hours). The h denotes the height (volume/surface) of the incubation chamber, and ρ is the density of seawater. Detailed benthic flux incubations and calculations are in the Supplementary Methods.

2.4. Statistical Analysis

Wilcox's robust analysis of variance was used to analyze seasonal and site-based variations in carbonate chemistry data. Due to skewed data in seagrass habitats, median comparisons over means were chosen (Baldry et al., 2020). The analysis was performed in R software v4.1.1.

3. Results

3.1. Carbonate Chemistry in Overlying Seawater

Generally, the carbonate chemistry parameters in the overlying seawater at DS and KT sites were distinctly different (Figure 2; Table S2 in Supporting Information S1). DS exhibited consistently higher pH than the SCS

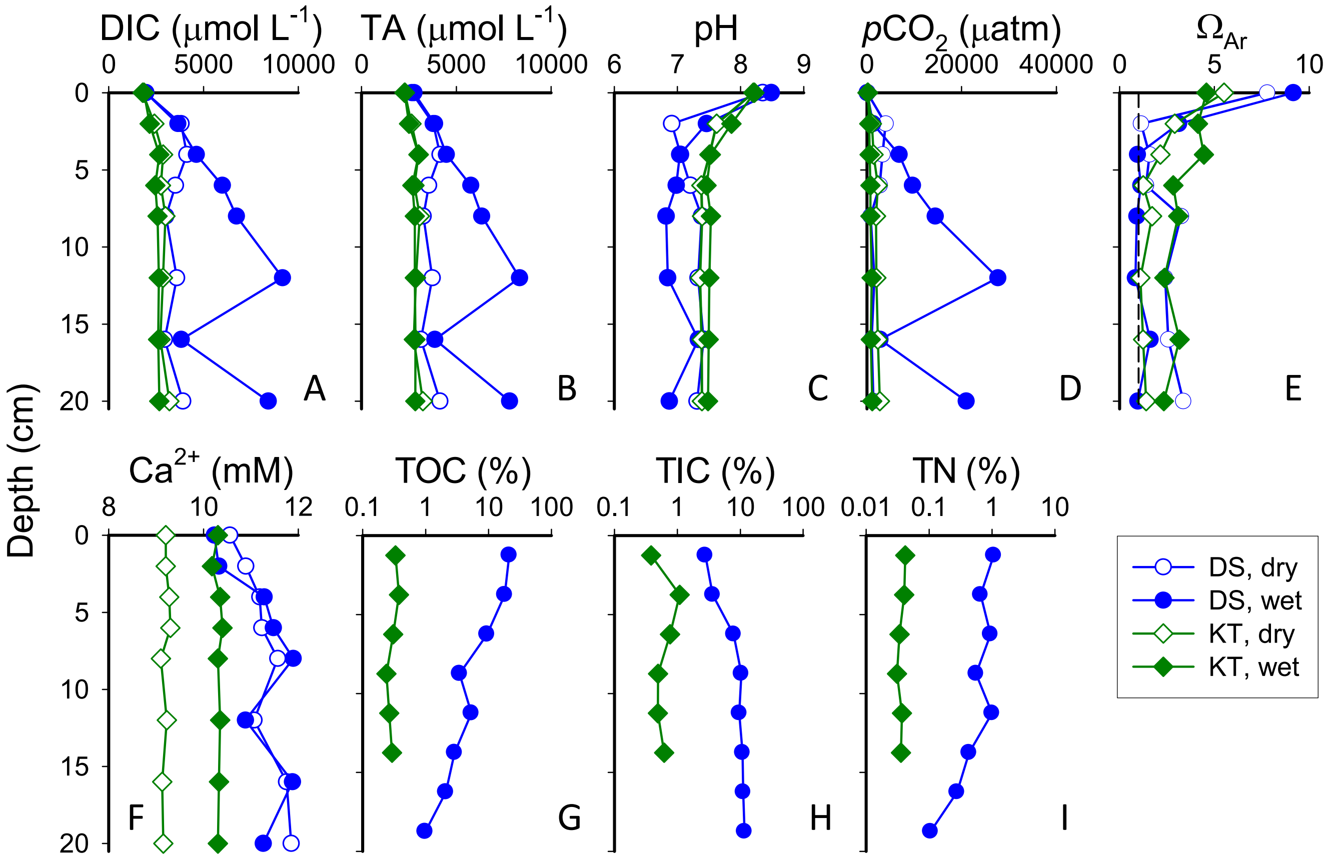

Figure 3. Vertical profiles of porewater dissolved inorganic carbon ,DIC, total alkalinity (TA), pH, pressure of CO_2, Ωar, and Ca^{2+}, and sediment profiles of Total organic carbon (TOC), total inorganic carbon (TIC), and total nitrogen (TN) in Dongsha (DS) and Kenting (KT) sites. Dry and wet seasons are denoted by open and solid symbols, respectively. The values of TOC, TIC, and TN contents are presented on a log scale. The unit "μmol/L" represents the total amount of DIC or TA in the interstitial water. The symbol "%" denotes the percentage dry weight of TOC, TIC, and TN. Vertical dashed line in E represents Ω_{Ar} equal to 1. DIC, dissolved inorganic carbon; TA, total alkalinity; TOC, Total organic carbon; TIC, total inorganic carbon; TN, total nitrogen.

average, indicating its potential to mitigate oceanic acidification, while KT slightly below this average suggesting limited mitigation potential (Figure 2a). A similar pattern was observed for Ω_{Ar}, which was consistently higher at DS than the SCS average, with KT fluctuating around it (Figure 2b). The pCO_2 at DS was significantly lower than at KT ($p < 0.05$) and below atmospheric levels, highlighting DS as a stronger carbon sink (Figure 2c; Supplementary Methods and Table S4 in Supporting Information S1). DIC values did not differ significantly between DS and KT, except for a deviation in KT during the dry season ($p < 0.05$, Figure 2d). In contrast, TA values were consistently higher at DS than KT (Figure 2e).

3.2. Carbonate Chemistry in Porewater

Vertical gradients in porewater exhibited sharper variations at DS compared to KT, and higher levels of DIC, pCO_2, and TA, and lower pH and Ω_{Ar} were observed at equivalent depths (Figures 3a–3f). Vertical gradients in porewater at DS showed sharper variations than at KT, with higher DIC, pCO_2, and TA, and lower pH and Ω_{Ar} at equivalent depths (Figures 3a–3f). At DS, maximum DIC, TA, and pCO_2 levels reached 9,164 μmol kg^{-1}, 8,339 μmol kg^{-1}, and 27,657 μatm, respectively, while at KT, they were lower at 3,193 μmol kg^{-1}, 3,229 μmol kg^{-1}, and 2760 μatm. pH and Ω_{Ar} decreased with depth, spanning from 6.82 to 8.49 and 0.84–9.16 at DS, and 7.36–8.22 and 1.09–5.51 at KT. Ca^{2+} concentrations were higher and more variable at DS (10.2–11.9 mM) compared to KT (9.1–10.4 mM), with a clear depth-related increase at DS, suggesting more intense $CaCO_3$ dissolution at this site.

3.3. Sediment Properties and Compositions

TOC, TIC, and TN levels in sediments differed notably between sites (Figures 3g–3i), with higher levels at DS (TOC: 1.0%–21.3%, TIC: 2.8%–11.7%, and TN: 0.11%–1.06%). In contrast, values at KT remained relatively constant and lower throughout the core (TOC: 0.24%–0.38%, TIC: 0.38%–1.09%, and TN: 0.031%–0.042%). Additionally, sediment grain characteristics and mineral compositions showed distinct differences between sites (see Text S2 and Fig. S4 in Supporting Information S1).

3.4. Benthic Fluxes of TA and DIC

The benthic fluxes of TA and DIC differed between the DS and KT seagrass meadows (Table S3 and Figure S5 in Supporting Information S1). At DS, the mean daily TA and DIC fluxes were 69.7 ± 40.7 and 107 ± 75.9 mmol m^{-2} d^{-1} for the dry season, and 75.8 ± 81.5 and 119 ± 144 mmol m^{-2} d^{-1} for the wet season, respectively (Fan et al., 2024). In contrast, the mean TA and DIC fluxes at KT were nearly two orders of magnitude lower. The TA and DIC estimates were 0.040 ± 0.066 and −0.084 ± 0.017 mmol m^{-2} d^{-1} for the dry season and 1.01 ± 1.40 and −0.016 ± 0.068 mmol m^{-2} d^{-1} for the wet season, respectively.

4. Discussion

Our results show notable differences in mineral composition and OC between sites. DS sediments primarily comprise preformed carbonate minerals (i.e., calcium carbonate minerals that have accumulated over geological time, such as those found in reef sediments) with high OC content, which is six times higher than the global average for seagrass meadows (15% vs. 2.5 wt%, Fourqurean et al., 2012). In contrast, KT sediments predominantly comprise terrestrial abiogenic minerals with relatively low OC content (0.38%). Consequently, higher porewater TA and Ca^{2+} concentrations at DS resulted in elevated benthic TA flux and concentration in the overlying seawater compared to KT. This evidence supports the notion that higher metabolic carbonate dissolution occurs in seagrass meadows at DS, and the resulting TA is transferred into the overlying seawater. Organic matter reactivity and quantity are crucial in biogeochemical processes. In organic-rich sediments, organic material can be both labile and recalcitrant. At the DS site, the high OC content in the 0–10 cm sediment layer likely includes a substantial portion of labile carbon available for aerobic respiration, which may drive carbonate dissolution and enhance alkalinity production. Over time, recalcitrant organic material can be exported or deposited in deeper layers, where it decomposes anaerobically through processes such as sulfate reduction and methanogenesis. The oxidation of hydrogen sulfide, produced by sulfate reduction, promotes carbonate dissolution, increasing TA, while methanogenesis supports carbonate precipitation (Meister et al., 2022). Enhanced sedimentary $CaCO_3$ dissolution has been documented in seagrass meadows in the Bahamas (Burdige & Zimmerman, 2002; Morse et al., 1985) and Florida Bay (Ku et al., 1999; Yates & Halley, 2006). The decreased pCO_2 and higher pH of the overlying seawater at DS further confirm that these seagrass meadows in reef sediments with high OC content can strengthen the carbon sink capacity of CBCEs and simultaneously mitigate ocean acidification through enhanced TA production (Chou et al., 2018).

A recent novel stochastic sediment biogeochemical model found that benthic TA flux can be approximately 10-fold higher in restored seagrass meadows with elevated concentrations of preformed $CaCO_3$ than those without (5.49 ± 2.21 vs. 0.52 ± 0.43 mmol m^{-2} d^{-1}; Fakhraee et al., 2023). The model outcomes unequivocally highlighted the favorable role of high $CaCO_3$ contents in promoting TA production. Our findings at KT (0.53 ± 0.99 mmol m^{-2} d^{-1}) corroborate the model predictions for seagrass meadows lacking preformed $CaCO_3$, while the results at DS (72.8 ± 64 mmol m^{-2} d^{-1}) substantially exceeded the model estimates for seagrass with high preformed $CaCO_3$ (Figure 4). This discrepancy could be due to the exceptionally high OC content at DS, which is located in a semi-enclosed lagoon where seagrass detritus export is hindered, causing an increase in OC loading in sediments. Similar patterns were seen in mangrove ecosystems, where TA fluxes are five-times higher in restored mangroves having elevated concentrations of preformed $CaCO_3$ compared to those without (Figure 4). Exceptionally high TA fluxes have been reported in mangrove forests on $CaCO_3$-rich sediments in the Red Sea region (Saderne et al., 2021). Additionally, generally higher TA fluxes are noted in mangroves than in seagrass meadows, possibly due to their higher OC loading (Alongi, 2014; McLeod et al., 2011). Collectively, these findings suggest that both elevated OC contents and $CaCO_3$ content may enhance TA production in CBCEs.

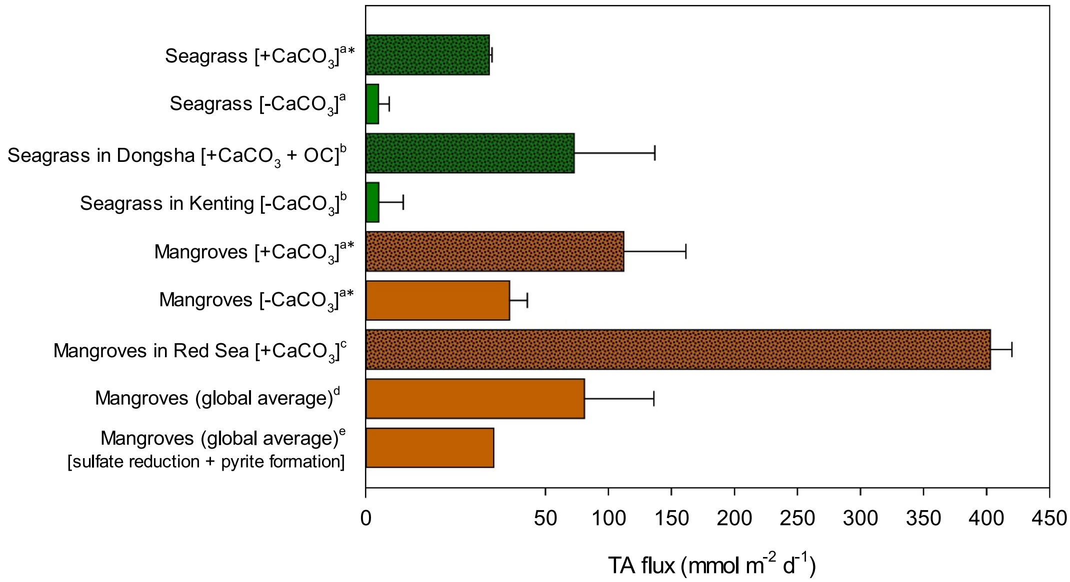

Figure 4. A comparison of benthic alkalinity fluxes (total alkalinity Flux) in coastal blue carbon ecosystems. Error bars represent ±1 standard deviation (σ). Data sources: [a] Fakhraee et al. (2023); [b] This study; [c] Saderne et al. (2021); [d] Reithmaier et al. (2021); [e] Reithmaier et al. (2023). An asterisk (*) indicates the modeled values.

To further estimate the translation of a net benthic TA flux into an increased air-sea flux of CO_2, we applied the approach used by Fakhraee et al. (2023) to estimate the alkalinity-driven atmospheric CO_2 uptake potential (see Text S3 in Supporting Information S1 for details). The estimated results show that the DS site had a higher alkalinity-driven CDR potential than KT based on the uptake efficiency approach, with seasonal averages of 9.56 ± 8.46 $tCO_2eq\ ha^{-1}\ y^{-1}$ at DS and 0.067 ± 0.13 $tCO_2eq\ ha^{-1}\ y^{-1}$ at KT (Renforth & Henderson, 2017). Global OC burial rate in seagrass meadows is 2.13 $tCO_2eq\ ha^{-1}\ y^{-1}$ (Duarte et al., 2013). At KT, the alkalinity-driven atmospheric CO_2 uptake potential was approximately 3% of the global OC burial rate, while it was 4.5 times higher at DS. A sensitivity analysis was futher conducted to assess the impact of a 100% error scenario on the CDR at KT and DS, compared to the global OC burial rate. While the CDR at DS varied more widely, this did not alter the finding that TA production at DS plays a significant role in carbon uptake. This first-order estimate again emphasizes the potentially critical role of TA fluxes in driving carbon uptake for seagrass growing on OC-rich reef sediments.

A conceptual diagram in Figure 5 illustrates the potential pathways of alkalinity generation through carbonate dissolution and/or sulfate reduction in seagrass meadows growing on OC-rich reef sediments. The enhanced oxygen availability facilitated by seagrass roots and rhizomes (i.e., radial oxygen loss; Jensen et al., 2005), along with an abundance of OC, promotes vigorous aerobic respiration. Elevated OC loading also promotes favorable conditions for sulfate reduction. The generated hydrogen sulfide (H_2S) further reacts with ferrous ions to form a pyrite precipitate (Fan et al., 2012). Alternatively, H_2S can readily undergo oxidation, particularly in zones exhibiting robust seagrass and mangrove growth, where sulfide oxidation processes are prevalent (Burdige, 2012; Burdige et al., 2008; Cai & Reimers, 1993; Cai et al., 2010). This oxidation process acts as a proton shuttle, decreasing pH (to 7.15 on the seawater scale) and increasing pCO_2 (Cai & Reimers, 1993; Ku et al., 1999). The resulting acidification, induced by increased aerobic respiration and sulfide oxidation, sharply reduces the $CaCO_3$ saturation state and drives its dissolution (Chou et al., 2021). Furthermore, the availability of abundant OC may enhance TA production through sulfate reduction coupled with pyrite formation (Reithmaier et al., 2021).

One limitation of our study lies in the partitioning of TA production from carbonate dissolution and sulfate reduction, as we did not quantify related parameters like sulfide concentration and sedimentary pyrite content. However, the estimated average global TA production coupled with pyrite formation in mangroves is 9.04 mmol m^{-2} d^{-1} (Reithmaier et al., 2021), being notably lower than the global average TA flux of

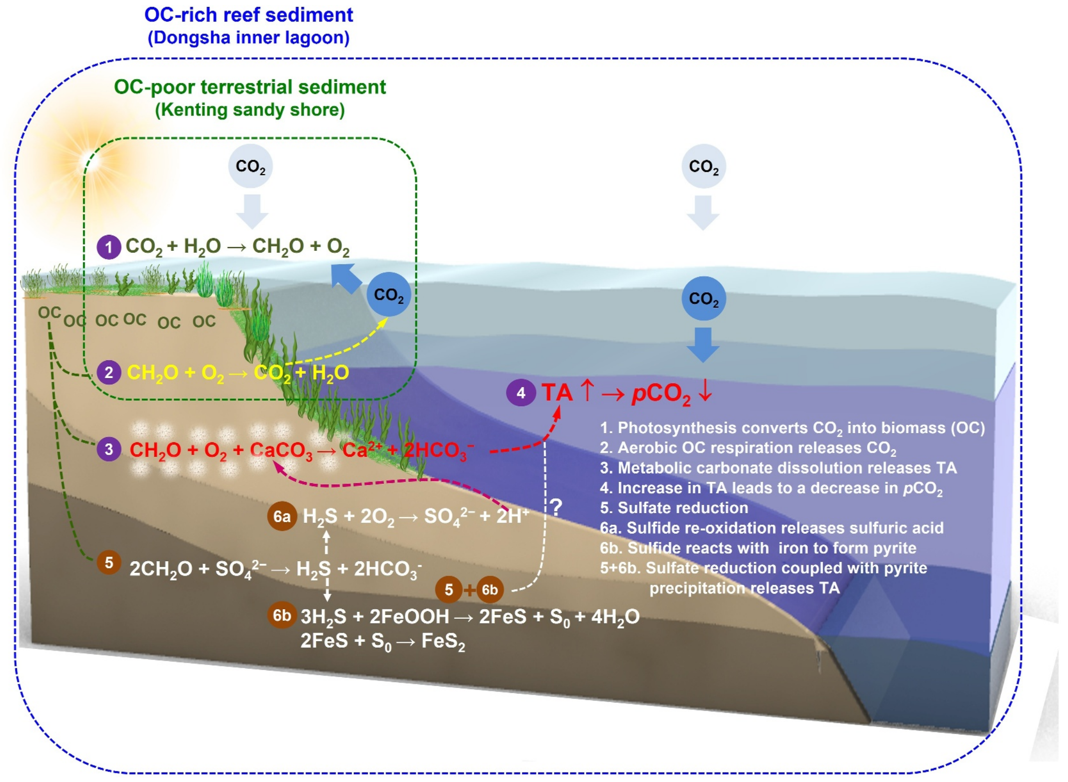

Figure 5. A diagram illustrating different carbon uptake processes in Dongsha (DS, blue frame) and Kenting (KT, green frame) sites. DS meadows feature additional pathways of total alkalinity generation via carbonate dissolution and/or sulfate reduction (in question mark as related parameters such as sulfide concentration and sedimentary pyrite content were not measured in this study), and represent an additional blue carbon sink.

81 ± 55 mmol m^{-2} d^{-1} in mangroves (Reithmaier et al., 2023) (Figure 4). Furthermore, the global average TA flux for restored mangroves with high quantities of preformed $CaCO_3$ was even higher (112.2 ± 49.3 mmol m^{-2} d^{-1}; Fakhraee et al., 2023). These findings imply that the metabolic carbonate dissolution may be more critical for TA production than sulfate reduction coupled with pyrite formation globally, at least for mangroves (Reithmaier et al., 2021). Current research on TA production in seagrass meadows is very limited, particularly regarding simultaneous measurements of inorganic carbon and sulfur cycling. Further investigation is needed on carbonate dissolution rates, sulfate reduction rates, sulfate and sulfide concentrations in porewater, and pyrite formation in sediments within seagrass meadows to distinguish the relative contribution of $CaCO_3$ dissolution and sulfate reduction in alkalinity generation.

5. Conclusions

Our findings reveal that the DS site, with high contents of preformed $CaCO_3$ and elevated OC content, exhibits a substantially higher benthic TA flux than the KT site, which primarily contains terrestrial sediments with low OC content. The elevated TA production at DS suggests enhanced metabolic carbonate dissolution and/or sulfate reduction, processes that promote greater uptake of atmospheric CO_2 and help mitigate ocean acidification. These findings highlight the importance of sediment properties in the CDR potential of CBCEs, which deserve further study.

Data Availability Statement

The data sets used in this study are available at Dryad Digital Repository via http://datadryad.org/stash/share/OMWUHYksFQ_esin47EX6c8L4CZu5lgjuJ83FY88gmew, with https://doi.org/10.5061/dryad.v41ns1s5x (Chou et al., 2024).

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