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Seagrass Abundance Predicts Surficial Soil Organic Carbon Stocks Across the Range of *Thalassia testudinum* in the Western North Atlantic

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Abstract

The organic carbon (C_{org}) stored in seagrass meadows is globally significant and could be relevant in strategies to mitigate increasing CO_2 concentration in the atmosphere. Most of that stored C_{org} is in the soils that underlie the seagrasses. We explored how seagrass and soil characteristics vary among seagrass meadows across the geographic range of turtlegrass (*Thalassia testudinum*) with a goal of illuminating the processes controlling soil organic carbon (C_{org}) storage spanning 23° of latitude. Seagrass abundance (percent cover, biomass, and canopy height) varied by over an order of magnitude across sites, and we found high variability in soil characteristics, with C_{org} ranging from 0.08 to 12.59% dry weight. Seagrass abundance was a good predictor of the C_{org} stocks in surficial soils, and the relative importance of seagrass-derived soil C_{org} increased as abundance increased. These relationships suggest that first-order estimates of surficial soil C_{org} stocks can be made by measuring seagrass abundance and applying a linear transfer function. The relative availability of the nutrients N and P to support plant growth was also correlated with soil C_{org} stocks. Stocks were lower at N-limited sites than at P-limited ones, but the importance of seagrass-derived organic matter to soil C_{org} stocks was not a function of nutrient limitation status. This finding seemed at odds with our observation that labile standard substrates decomposed more slowly at N-limited than at P-limited sites, since even though decomposition rates were 55% lower at N-limited sites, less C_{org} was accumulating in the soils. The dependence of C_{org} stocks and decomposition rates on nutrient availability suggests that eutrophication is likely to exert a strong influence on carbon storage in seagrass meadows.

Keywords Blue carbon · Submerged aquatic vegetation · Latitudinal gradients · Decomposition · Nutrient limitation · Sediment

Introduction

Seagrass beds are hot-spots for organic carbon (C_{org}) burial in the oceans (Duarte et al. 2005) and store as much carbon per hectare as many terrestrial forests ecosystems (Fourqurean et al. 2012b). Unlike terrestrial forests, where the C_{org} stores are dominated by living aboveground biomass (Keith et al. 2009), the C_{org} stores of seagrass meadows are dominated by carbon below ground in their organic-rich soils (Duarte et al. 2005; Fourqurean et al. 2012a; McLeod et al. 2011). Consequently, factors that determine the C_{org} content and accumulation rates in soils will control the size of seagrass carbon stocks. Important among these factors are the abundance and productivity of the seagrasses and other associated primary producers (Serrano et al. 2014), the rate of decomposition of biomass deposited (Howard et al.

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2021), and the depositional/erosional environment within the seagrass canopy (Hansen and Reidenbach 2012).

Seagrass biomass, canopy structure, carbon production, and species composition are often influenced by nutrient availability (Carruthers et al. 2007; de Boer 2007; Duarte 1995; Fourqurean et al. 1992; Hughes et al. 2004; Short 1987), as well as other factors such as light availability, grazing by herbivores, and wave energy. Seagrass biomass, canopy structure, and species composition, in turn, influence the depositional environment in the meadow (de Boer 2007; Fonseca and Fisher 1986; Ford et al. 2001; Gacia and Duarte 2001; Koch 1999; Madsen et al. 2001) and therefore C_{org} deposition in soils (Samper-Villarreal et al. 2016).

Many factors can limit the abundance and productivity of seagrasses, including light availability (Dennison 1987), environmental stress (Koch et al. 2013), herbivory (Heck and Valentine 2006; Nowicki et al. 2018), and nutrient availability (Lee et al. 2007). In nutrient-limited seagrasses, nutrient addition increases primary productivity and biomass of plants, thereby increasing the rate of organic matter (OM) production, increasing trapping of allochthonous carbon, and preventing erosion of deposited carbon (Gacia et al. 2002; Hemminga et al. 1991; Madsen et al. 2001). Whether nutrient-limited seagrasses are limited by nitrogen (N), phosphorus (P), or some other resource is imperfectly predicted by the mineralogy of the soils in which they grow: many, but not all, seagrasses in carbonate soils are P-limited (Fourqurean and Zieman 2002; Short 1987) while those in siliceous soils tend to be N-limited (Short 1987). Hence, mineralogy of soils could influence the mechanisms by which changing nutrient availability influences seagrass carbon stores, and nutrient availability may also influence the balance between autochthonous and allochthonous organic carbon that is deposited in soils.

Seagrass ecosystems preserve soil OM by creating relatively stable, low redox, anoxic soil environments that limit microbial activity, and impede remineralization (Duarte et al. 2011; Fourqurean et al. 2012a; Trevathan-Tackett et al. 2018) and decomposition rates are generally a function of temperature so that decomposition is slower in cooler, less tropical environments. Across sites with suitable temperature ranges for seagrasses, factors that influence seagrass soil conditions, like seagrass abundance, could therefore influence the decomposition rate of soil OM. The organic component of soils underlying seagrass meadows consists of a diverse mixture of particles and macromolecules that vary in their resistance to remineralization (Burdige 2007; Howard et al. 2021). The decomposition of recalcitrant soil C_{org} is enhanced by labile organic inputs (Trevathan-Tackett et al. 2018), and decomposition can be accelerated in areas with higher nutrient availability (Armitage and Fourqurean 2016). Further, the constituents of soil C_{org} vary spatially and temporally, determined by the source and type of OM inputs, as well as the degree and milieu of processing (Arndt et al. 2013; Burdige 2007; Howard et al. 2021). Because of the variability in OM quality and environmental conditions across sites, comparison of potential decomposition rates across diverse sites necessitates the measurement of the decomposition of standardized substrates like canvas strips and tea bags (Howard et al. 2021; Keuskamp et al. 2013; Tiegs et al. 2007).

A proportion of the C_{org} that accumulates in seagrass meadows derives from direct production of seagrass biomass. The belowground production of roots and rhizomes creates already-buried OM, which remains in the soils both during and after the lifespan of the plants. Further, belowground seagrass biomass also exude dissolved OM into the soils (Li et al. 2021). Aboveground production of leaf tissue adds OM to soils indirectly as leaves naturally break off the plant shoot and accumulate on the soil surface, leading to their eventual burial (Duarte and Cebrián 1996). Alongside this direct source of carbon from seagrass tissues, organic matter from other sources, such as terrestrial runoff and suspended particulate organic matter, accumulates in the sediments due to the seagrass canopies acting as efficient filters, stripping particles from the water column, and adding them to the sediment load (Hendriks et al. 2008). As a result of these processes, there is a net transfer of allochthonous carbon to the sediments of seagrass meadows that enhances their capacity for long-term carbon sequestration, but the relative proportions of allochthonous to autochthonous C_{org} buried in seagrass soils can vary depending on rates of autochthonous C_{org} production, depositional environment, and relative availability of allochthonous sources. Globally, stable C isotope mixing models suggest that an average of ca. 51% of the C_{org} in seagrass soils is derived from production in the seagrass meadow, with half of meadows having between 33 and 62% contribution of seagrass meadow-derived C_{org} (Kennedy et al. 2010); further, there is an influence of seagrass species composition on the importance of allochthonous C_{org} buried in seagrass soils, likely due to species-specific differences in above- and belowground biomass and canopy structure which influence interactions with the water column (Kennedy et al. 2022).

Disentangling the relationships among seagrass abundance, nutrient availability, and organic matter provenance and decomposition rates on the soil C_{org} stores of seagrass meadows requires controlled experiments and/or systematic surveys across the geographic range of a single species. As a first step toward understanding these relationships, we explored the variation in soil characteristics, soil C_{org} stores, nutrient availability, and decomposition rates at 13 sites that cover the entire geographical range of seagrass meadows dominated by *Thalassia testudinum* in the western North Atlantic Ocean. Specifically, we tested the hypotheses that, across the range of the

species, (1) seagrass soil C_{org} increases as a function of seagrass abundance, (2) nutrient-limited seagrass meadows have lower soil C_{org} stores than nutrient-replete ones, (3) phosphorus-limited seagrasses are associated with carbonate sediment, (4) high seagrass abundance leads to a higher proportion of autochthonous C_{org} in the soil, and (5) organic matter decomposition rates in the seagrass soil are influenced by site average temperature, nutrient availability, and seagrass abundance.

Methods

The work described here is a component of a larger coordinated and distributed research program, the Thalassia Experimental Network (TEN) conducted at 13 sites in the western North Atlantic (Fig. 1) that span the geographic range of turtlegrass (*Thalassia testudinum*), and sites were purposely chosen to exploit tropical-subtropical gradients (9–32° N) in temperature and photoperiod. At each network site, the specific location for the experiment was selected by adhering to a standardized set of criteria, including similar depths (< 4 m), in seagrass beds dominated by *T. testudinum* (> 50% relative abundance *T. testudinum*, although some sites had other species like *Syringodium filiforme* as components of the seagrass community), areal extent of bed (> 25 × 25 m), and low wave energy and storm exposure. The major TEN experiment was a factorial manipulation of nutrient addition and altered herbivory which ran for approximately one year (experimental work at individual sites was initiated between April and June 2018; see Campbell et al. In review). For this study, we collected samples from unmanipulated control plots at each site in spring–summer of 2019 and organic matter decomposition rates measured over an approximately 4-month period at the beginning of the experiment.

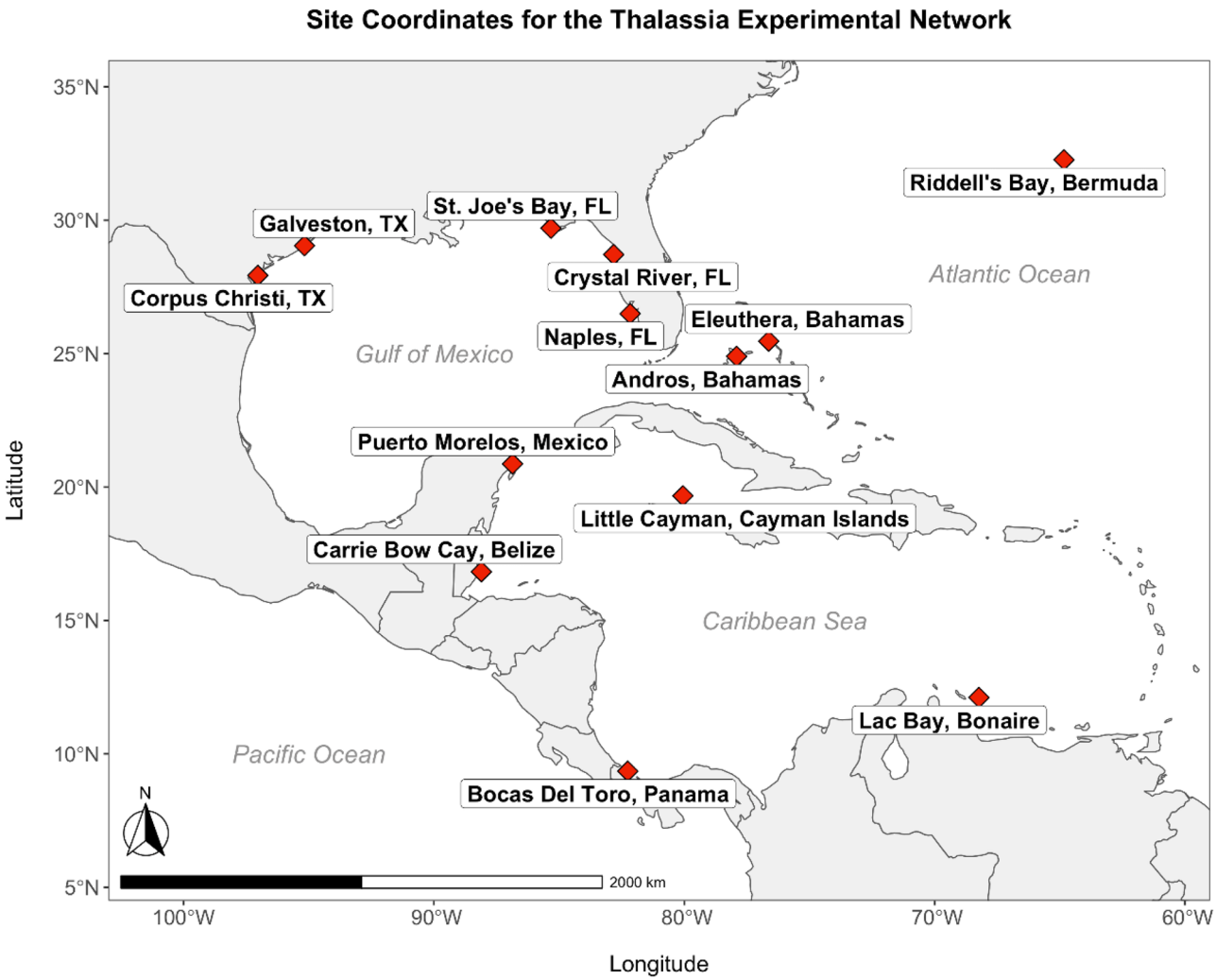

Fig. 1 Map of experimental sites

Assessing Seagrass Abundance and Canopy Height

Five unmanipulated, 0.25-m^2 plots were established in a larger grid of experimental plots within a 15 × 25 m array at each site as part of the TEN experiments. Four shoots from each plot were collected, and canopy height was determined as the average leaf length. Shoot density was determined by counting shoots within two replicate 15-cm-diameter rings in each plot. *Thalassia testudinum* plants were collected with a 15-cm-diameter corer inserted to a depth of 20 cm for determination of aboveground biomass (AGB) and leaf nutrient (C, N, and P) content. Cores were washed free of sediments using mesh bags, and remaining seagrass biomass was returned to the laboratory. Green leaf material was separated from belowground material, and epiphytes and other particles were removed from the green leaves by gentle scraping using razor blades. Leaf length was measured for length to the nearest mm. Above and belowground biomass (BGB) samples were dried to a constant weight at 50 °C, and leaf material was homogenized to a fine powder using a motorized ball mill for subsequent analyses.

Sampling Soil Properties

We sampled the soils using cut-off 60-mL polyethylene syringes modified into piston corers that allowed for collection of the top ~10 cm of surficial soil without compaction. Core volume was recorded, and soil samples were transferred to pre-weighed vessels and dried to constant weight at 50 °C. We calculated dry bulk density (DBD, in g mL^{-3}) as mass of dry sample/core volume. Large (> 3 mm) pieces of seagrass and macroalgae were removed from the dry soil material, and the remaining sample was homogenized using a motorized ball mill.

Elemental Analyses of Seagrasses and Soils

Subsamples of dry, homogenized seagrass leaves were analyzed for total phosphorus (TP) content using a dry oxidation-acid hydrolysis procedure (Fourqurean et al. 1992) and for total carbon (TC) and total nitrogen (TN) using an elemental analyzer (Thermo Flash 1112). While there are large ranges in elemental content plant tissues driven by many factors, tissue nutrient concentrations are often used to assess the relative availability of different nutrients. For *T. testudinum* the critical N:P molar ratio of roughly 30:1 suggests a balance of N and P supply for growth while deviations from 30:1 can be used to assess either N limitation (N:P < 30) or P limitation (N:P > 30) (Armitage et al. 2005; Atkinson and Smith 1983; Duarte 1992; Fourqurean and Rutten 2003).

Subsamples of the homogenized soils were analyzed for organic matter (OM) content by loss on ignition for 4 h at 500 °C. Other subsamples were analyzed for TC, TN, and TP using the procedures described above for seagrass leaves. We measured soil C_{org} content using a combination loss-on-ignition/elemental analyzer method (Fourqurean et al. 2012b). Inorganic C content (C_{inorg}) was calculated as TC − C_{org}. Note that a soil composed of 100% calcium carbonate particles would have a $C_{inorg} \approx 12\%$ C_{inorg} by dry weight. We assumed that the mass of soils remaining after subtracting the OM and carbonates was an indicator of siliciclastic sediments. C_{org} density was calculated as the product C_{org}•DBD. All elemental ratios were calculated on a mol:mol basis.

Stable C Isotope Composition of Seagrass Leaves and Soil C_{org}

The $\delta^{13}C$ and $\delta^{15}N$ values for dry seagrass leaf samples, and the $\delta^{13}C$ for soil organic matter, were determined using an EA-IRMS. Since the soil samples contained appreciable C_{inorg} in the form of carbonates, subsamples of dry, homogenized soil and seagrass leaves were fumed with HCl for a minimum of 14 days until a constant weight was reached to remove C_{inorg}, and the $\delta^{13}C$ of the C_{org} in the samples was measured. An elemental analyzer was used to combust these samples to convert C_{org} to CO_2, which was then measured on a Finnigan MAT Delta C IRMS in a continuous flow mode. Stable isotope values were reported in the standard delta notation with respect to the international standard Vienna Pee Dee Belemnite (‰). Analytical reproducibility of the reported values, based on sample replicates, was better than ±0.08‰.

Determining Provenance of Soil C_{org}

We calculated soil $\Delta^{13}C$ for each site, the difference between site-averaged $\delta^{13}C$ of soil and seagrass leaves, to assess the contribution of allochthonous OC to the soils (Kennedy et al. 2010). To explore the likely fractional contribution of possible sources of C to the soil C_{org}, we developed Bayesian stable isotope mixing models (Eq. S1) using the R package MixSIAR v.3.1.12 (Stock et al. 2018). We calculated the proportional contribution of endmembers seagrass, phytoplankton, and mangrove/terrestrial organic matter to the sediment organic carbon pool using $\delta^{13}C$ as tracer. Site-specific seagrass endmember $\delta^{13}C$ values were derived from local data for each site, while literature values were used for phytoplankton (−20 ± 2‰0; (Goericke and Fry 1994) and mangrove organic matter (−28.2 ± 1.2‰); (Bouillon et al. 2008) due to a lack of local data. The latter endmember is indistinguishable from terrestrial organic matter (−28.46 ± 2.52‰); (Diefendorf et al. 2010), and we thus did not differentiate terrestrial and mangrove-derived C_{org}. Our mixing models used informative priors, assuming seagrass material contributed 50% of sedimentary organic matter following

(Kennedy et al. 2010), with the other endmembers contributing equally. Sensitivity analysis revealed that uninformative priors did not produce diverging estimates. Separate mixing models were developed for each site and included a residual error term (Parnell et al. 2010). In addition, a global model was developed using the mean and standard deviation of all seagrass $\delta^{13}C$ sample data to estimate proportional contributions of endmembers to soils across all study sites. Markov Chain Monte Carlo parameters were set as follows: chains = 3; chain length = 1,000,000; burn = 500,000; thin = 500. Model convergence was evaluated using Geweke as well as Gelman-Rubin diagnostics (Table S3).

Organic Matter Decomposition Rates

We deployed standardized plant substrates, in the form of commercial tea bags (Keuskamp et al. 2013), ca. 9 cm into the soil in each plot at all sites except for Puerto Morelos. Two kinds of tea bags, green and rooibos tea ($n = 65$ each for rooibos and green teas), were deployed. The green tea is a more labile substrate for decomposition compared to the rooibos tea (Trevathan-Tackett et al. 2020). The dry mass of each tea bag was measured before deployment. After approximately 4 months, the tea bags were excavated from the plots, washed clean of adhering sediment in freshwater, and dried. Retrieval success after 4 months varied among sites. Tea bags from one of the sites (Eleuthera) were damaged and did not provide reasonable data, and bags from the Corpus Christi site were incubated for more than twice as long as the other sites so those data were not included in the analyses. Of the 130 originally deployed tea bags, 36 rooibos tea and 25 green tea bags from the remaining 10 sites were recovered in a state that allowed for further processing. Note that these decomposition bags were only deployed during the summer/fall months (ca. April 2018–October 2018) when temperature variation among sites was minimal to test the effect of site characteristics (e.g., C_{org} content, nutrient levels, and organic content of soil) independently of temperature given the widely acknowledged effects of temperature on decomposition. For both kinds of tea, the net weights of the dry tea at the beginning of the experiment ($W_{initial}$), based on a subset of representative teabags and the weights after d days (W_{final}) were used to calculate an effective exponential decay rate k (in units of % day^{-1}):

$$k = -\left(\frac{lnW_{final} - lnW_{initial}}{d}\right) \times 100\%$$

Subscripts on k indicate the type of tea (k_r for rooibos tea or k_g for green tea).

We analyzed the differences in soil and seagrass characteristics among sites by comparing means of replicates at each site with ANOVA, and we explored intra-site differences using Student–Newman–Keuls post hoc tests. We tested for differences in decomposition rates of different tea types using a paired sample T-test, with substrates paired within sites. All error bars and confidence intervals are given as ± 1 standard error. For exploring pairwise relationships between variables, we used bivariate correlation analyses and linear regression.

Results

Seagrass Meadow Characteristics Across Sites

The abundance and characteristics of *Thalassia testudinum* varied widely across the 13 sites. Individual plots had shoot densities that ranged over 2 orders of magnitude and total plant biomass that ranged over 3 orders of magnitude (Supplemental Table S1). Similarly, plant stature also varied across the sites; the average leaf length within plots ranged from 12 to 276 mm. Seagrass density, above- and belowground biomass, and leaf length varied among sites (Fig. 2, ANOVAs for individual measures of abundance, $n = 5$ replicates per site, all $F > 10.14$; all $p < 0.001$ at $\alpha = 0.05$). Abundance was higher at the Bonaire, Carrie Bow, Cayman, Andros, and Crystal River sites compared to the remaining sites, but there was no latitudinal gradient in abundance.

Seagrass nutrient content also varied greatly (Supplemental Table S1). Phosphorus content of leaf tissues varied from 0.049 to 0.388%. Variation in N content was substantial but not as great, with values ranging from 1.21 to 4.36%. There were clear differences in elemental content and ratios among sites (Fig. 3; ANOVAs for individual response variables, $n = 5$ replicates per site, $F > 14.0$ for all comparisons, all $p < 0.001$ at $\alpha = 0.05$). Post hoc analyses (Student-Newman-Kuels, $\alpha = 0.05$) pointed to some general groupings of sites based on seagrass nutrient content. As indicated by P content (% of dry wt) and ratios of C:P and N:P, relative P availability was lowest at the Cayman, Puerto Morelos, Andros, and Eleuthera sites. Nitrogen content was particularly high at the more northerly and some Gulf of Mexico sites (e.g., Naples, Corpus Christi, and Galveston) and Bermuda. Seagrass leaf N:P exhibited a wide range of values across sites (ANOVA, $F_{12,53} = 13.990$, $\alpha = 0.05$, $p < 0.001$), indicating large differences in the relative availability of N and P to support seagrass growth. Site-specific means ranged from 23.7 ± 1.4 at Galveston to 55.1 ± 5.3 at Puerto Morelos (Fig. 6). The Naples, Corpus Christi, Galveston, and Bocas del Toro sites had mean values < 30, suggesting seagrass N-limitation, while the Puerto Morelos, Cayman Islands, Andros, and Eleuthera sites had N:P values > 30, suggesting P-limitation. Mean values for Bermuda, Bonaire,

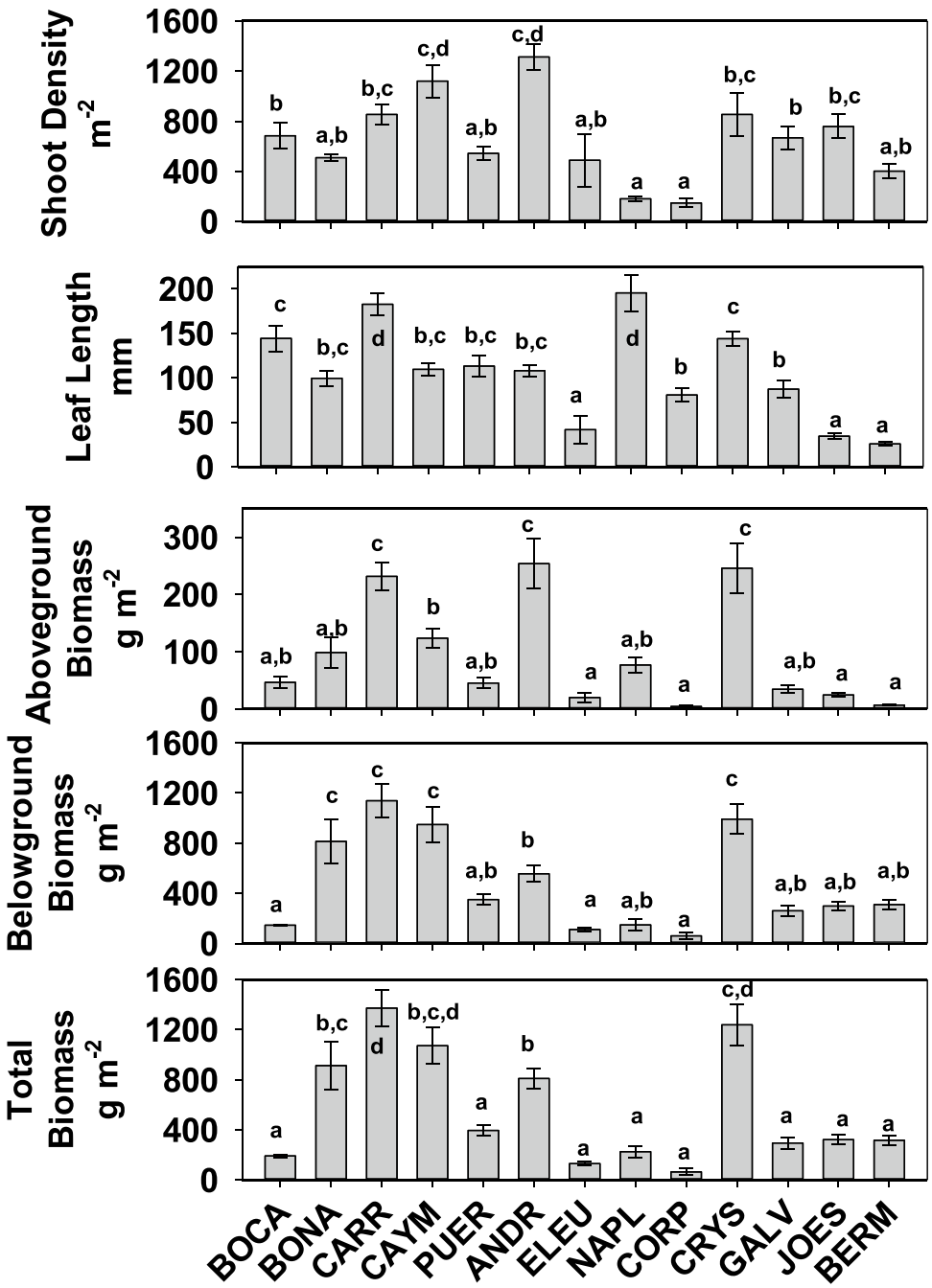

Fig. 2 *Thalassia testudinum* abundance and leaf length at the 13 study sites, with sites ordered by increasing latitude from left to right. Error bars indicate ± 1 SE. ANOVA indicated differences in means of all properties among sites ($p < 0.001$ for all comparisons), and letters designate homogenous subsets of sites for each soil property (S-N-K post hoc tests at $\alpha = 0.05$). Site abbreviations: BOCA, Bocas del Toro, Panama; BONA, Lac Bay, Bonaire; CARR, Carrie Bow Cay, Belize; CAYM, Little Cayman, Cayman Islands; PUER, Puerto Morelos, Mexico; ANDR, Andros, Bahamas; ELEU, Eleuthera, Bahamas; NAPL, Naples, Florida, USA; CORP, Corpus Christi, Texas, USA; CRYS, Crystal River, Florida, USA; GALV, Galveston, Texas, USA; JOES, St. Joseph Bay, Florida, USA; BERM, Riddell's Bay, Bermuda

Crystal River, St. Joseph Bay, and Carrie Bow Cay were very close to 30, suggesting some factor other than availability of N or P was limiting seagrass growth.

Soil Characteristics Across Sites

Soil characteristics varied broadly across sampling sites (Supplemental Table S2). Soil samples across all sites had DBD values from 0.18 to 1.42 mg mL^{-1}, with a median value of 0.83 mg L^{-1}. DBD values had a non-normal distribution and displayed three groups with modal values of 0.2–0.3, 0.8–0.9, and 1.2–1.3 mg mL^{-1} ($n = 56$, Supplemental Fig. S1). These DBD values are consistent with one set of samples from highly organic sites with the lowest values of DBD, a larger set of samples from carbonate-based soil sites with intermediate DBD values, and a third set of samples from sites with siliceous soils at higher DBD. There was a similarly broad and non-normal, bimodal distribution of soil carbonate content (inorganic C, C_{inorg}), with a range of 0–11.2% of dry weight with a median of 10.0% of dry

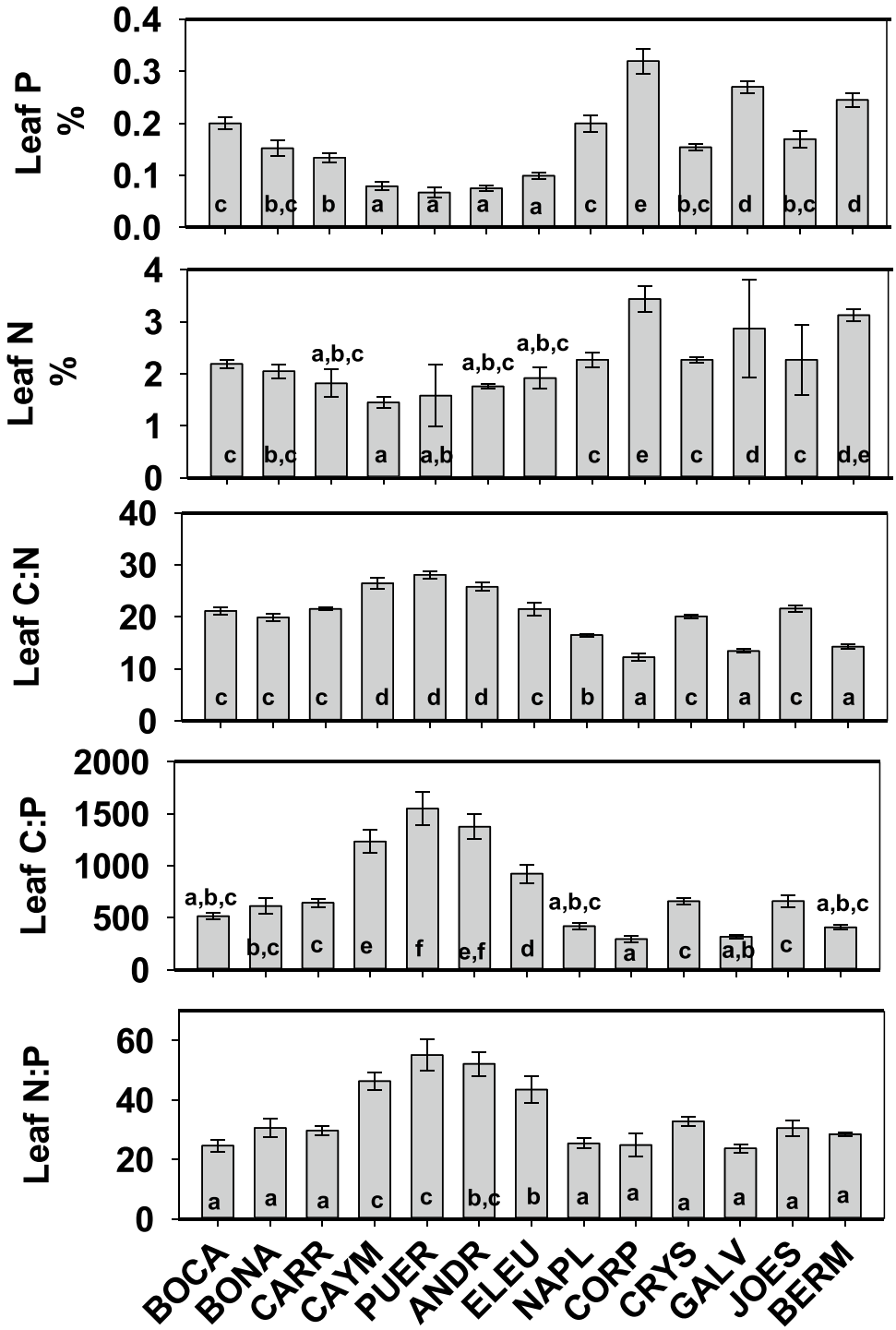

Fig. 3 *Thalassia testudinum* leaf nutrient content from the 13 study sites, ordered by increasing latitude from left to right. N and P contents are given as % of dry weight, and ratios are calculated on a mol:mol basis. Error bars indicate ± 1 SE. ANOVA indicated differences in means of all properties among sites ($p < 0.001$ for all comparisons), and letters designate homogenous subsets of sites for each soil property (S-N-K post hoc tests at $\alpha = 0.05$). Site abbreviations: BOCA, Bocas del Toro, Panama; BONA, Lac Bay, Bonaire; CARR, Carrie Bow Cay, Belize; CAYM, Little Cayman, Cayman Islands; PUER, Puerto Morelos, Mexico; ANDR, Andros, Bahamas; ELEU, Eleuthera, Bahamas; NAPL, Naples, Florida, USA; CORP, Corpus Christi, Texas, USA; CRYS, Crystal River, Florida, USA; GALV, Galveston, Texas, USA; JOES, St. Joseph Bay, Florida, USA; BERM, Riddell's Bay, Bermuda

weight ($n = 64$). Samples were clustered into three groups, with most observations having either very low or very high carbonate content, with a smaller number of sites displaying intermediate carbonate contents. In contrast, C_{org} contents varied from 0.11 to 10.5% by dry weight ($n = 64$) with a median value of 1.4% by dry weight with a truncated normal distribution and relatively few high values. Observations of C_{org} density, the product of C_{org} content and DBD, were normally distributed with a mean of 12.5 ± 0.9 mg C_{org} mL^{-1} and a median value of 11.8 mg C_{org} mL^{-1} ($n = 56$).

Phosphorus content of the soil samples ranged from 0.003 to 0.111% with a mean of 0.021 ± 0.001% by dry weight ($n = 64$, Fig. 4, Supplemental Fig. S2 and Table S2). Nitrogen was more abundant in general, with values ranging from 0 to 1.05% with a mean of 0.20 ± 0.01% ($n = 64$). The distribution of observations of both N and P content was dominated by low

values, with relatively few observations of high values. Soil C_{org}:N ratios were normally distributed, with a range from 2.5 to 32.4 and a mean of 11.3 ± 0.2 (n = 64). Driven by the distribution of soil P content, both C_{org}:P and N:P were skewed toward low values with relatively few high values. C_{org}:P ranged from 11.2 to 1347.1 with a median of 264.0 (n = 64) and N:P ranged from 0 to 217.3 with a median value of 26.6 (n = 64).

There were also distinct groupings of sites according to soil parameters (Fig. 4; ANOVA, n = 5 replicates per site, $p < 0.001$ for all comparisons). Post hoc analyses (Student-Newman-Kuels, $\alpha = 0.05$) showed that sites grouped into subsets with similar values for the different soil parameters. In general, northerly, continental sites (Naples, Corpus Christi, Galveston, and St. Joseph Bay) had high DBD and low C_{org} and C_{inorg}, indicating that their soils were composed

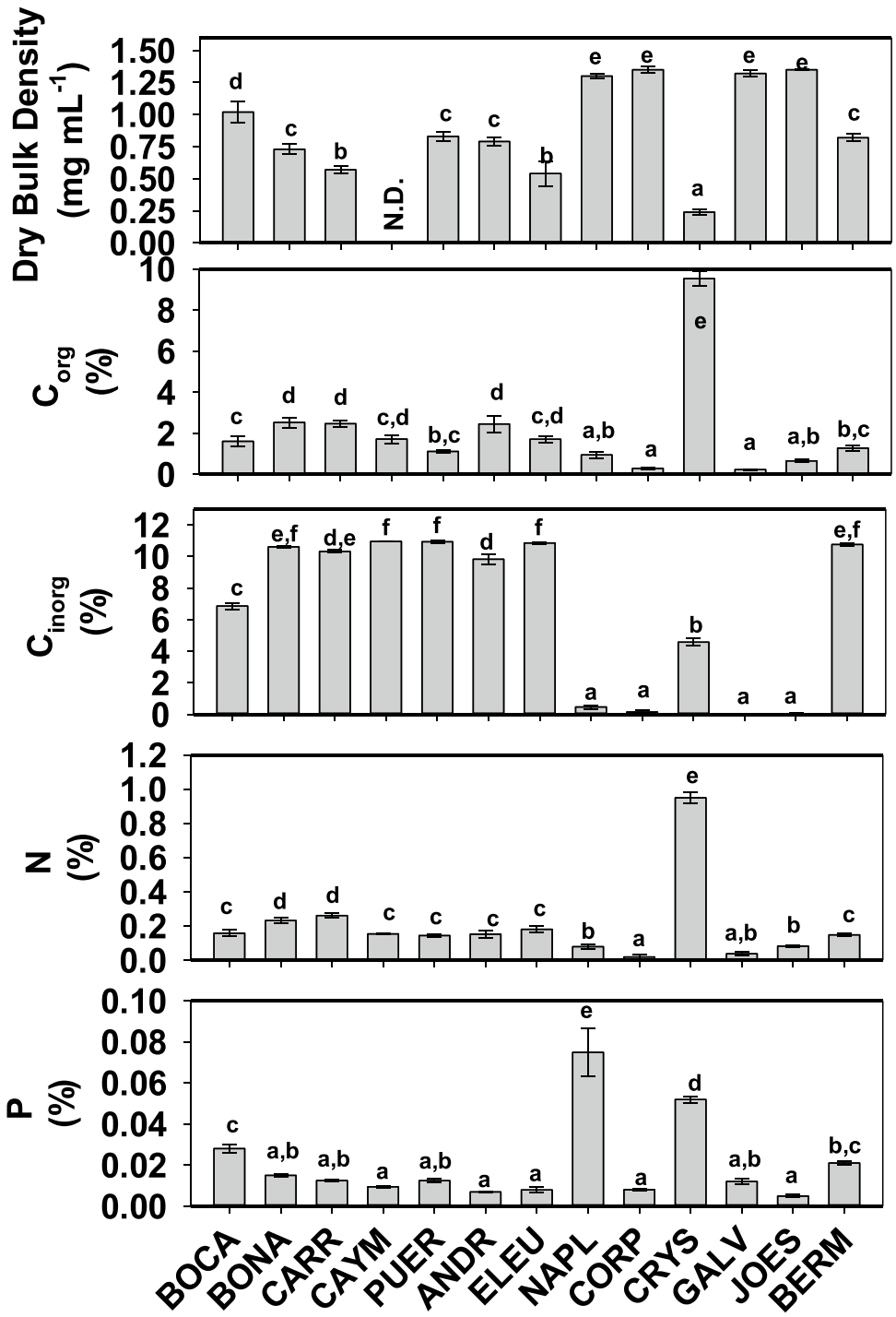

Fig. 4 Soil properties at the 13 study sites, ordered by increasing latitude from left to right. Error bars indicate ± 1 SE. ANOVA indicated differences in means of all properties among sites ($p < 0.001$ for all comparisons), and letters designate homogenous subsets of sites for each soil property (S-N-K post hoc tests at α = 0.05). No data (N.D.) indicates missing dry bulk density data from the Cayman Islands and Crystal River sites. Site abbreviations: BOCA, Bocas del Toro, Panama; BONA, Lac Bay, Bonaire; CARR, Carrie Bow Cay, Belize; CAYM, Little Cayman, Cayman Islands; PUER, Puerto Morelos, Mexico; ANDR, Andros, Bahamas; ELEU, Eleuthera, Bahamas; NAPL, Naples, Florida, USA; CORP, Corpus Christi, Texas, USA; CRYS, Crystal River, Florida, USA; GALV, Galveston, Texas, USA; JOES, St. Joseph Bay, Florida, USA; BERM, Riddell's Bay, Bermuda

of primarily siliciclastic sediments. The fifth temperate continental site, Crystal River, differed in having relatively high C_{org} (9.5 ± 0.4%), low DBD (0.24 ± 0.02 mg mL^{-1}), and appreciable carbonate sediments (C_{inorg} = 4.6 ± 0.2%). Soils from the Bocas del Toro site were also a mix of siliciclastic and carbonates, while soils from the remaining seven sites were composed chiefly of carbonate sediments. Soils from the Crystal River site had much higher organic content than the other 12 sites which had mean C_{org} concentrations between 0.2 and 2.5%. The Crystal River site also had much higher soil N content (0.94 ± 0.03%) than the other sites, which all had N content < 0.27%. Two sites (Naples and Crystal River) had much higher soil P content (> 0.06% P) than the other 11, which were all below 0.028% P. The Bocas del Toro and Bermuda sites had intermediate soil P content (0.028 ± 0.002% and 0.021 ± 0.001%, respectively). The remaining 9 sites all had soil P content < 0.015 ± 0.001%.

Site-specific differences in soil characteristics were not simply explained by latitude (Fig. 4) or by temperature differences across the latitudinal range of our sites (Supplemental Fig. S4). Sites with lower average annual temperatures occurred at higher latitudes, where there was a greater annual temperature range, so that these mean temperatures covaried with latitude (Spearman's rank = −0.88, Supplemental Fig. S3). The coolest annual mean was 22.5 ± 7.3 °C at Galveston, and the warmest annual mean was 29.7 ± 0.01 °C at Bocas del Toro. While there was a tendency for higher-latitude, more seasonal, and cooler sites to have lower C_{org} and soil N (but not P) content, our more temperate Crystal River site was a strong outlier with the highest soil C_{org} and N content (Supplemental Fig. S4).

Comparisons of Seagrass and Soil Nutrient Content Across Sites

Soil and leaf nutrients were not highly correlated with one another, but they were correlated with certain soil and leaf characteristics. Specifically, relative abundance of N and P in the soil and seagrass leaves were poorly correlated, suggesting that soil N and P relative abundance was an imperfect predictor of the nature of nutrient limitation at a site (Fig. 5). DBD was correlated with higher soil C_{inorg}, C_{org}, and N content, but P was not correlated with DBD (Table 1). C_{org} was positively correlated with P and N content, and N and P were also positively correlated. While there was a general increase in seagrass leaf N:P as soil N:P increased, there was a group of sites (Crystal River, St. Joseph Bay, and Carrie Bow) with relatively high soil N:P with seagrass leaf N:P near 30:1, suggesting that some other factor other than soil nutrient concentrations was influencing relative rates of incorporation of N and P by the plants. The abundance of carbonates in the soil, or C_{inorg}, did not correctly predict the nature of nutrient limitation for *Thalassia testudinum* across the sites (Fig. 6). At the Carrie Bow, Bonaire, and Bermuda sites, N:P of leaves indicated balanced supply of N and P to support growth even in carbonate-rich sediments.

Relationships Between Seagrass Abundance and Soil Organic C Content

Site-averaged soil C_{org} content and C_{org} density were both influenced by seagrass abundance (Fig. 7). Soil C_{org} content increased by 0.017 ± 0.006% for every gram increase in

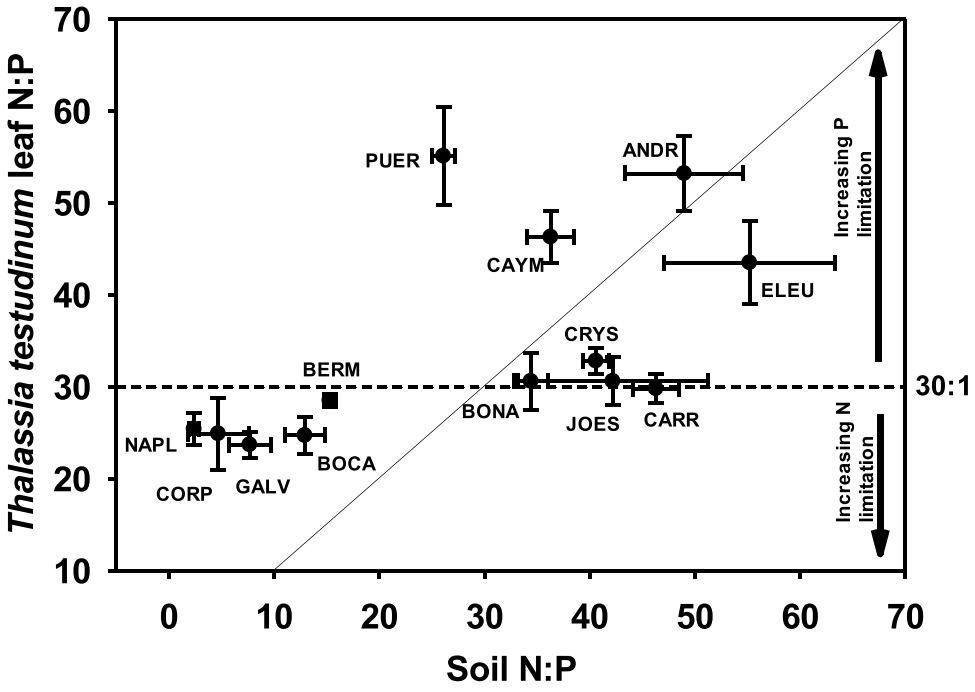

Fig. 5 Relationship between site-averaged seagrass leaf N:P and soil N:P stoichiometry. Error bars indicate ± 1 SE. Diagonal line represents the 1:1 relationship. Seagrass leaf N:P > 30 indicates P limitation, N:P < 30 indicates N limitation, and N:P ≈ 30 suggests some other limiting factor. See Fig. 4 caption for site abbreviations

Table 1 Correlation among soil properties at plot level

	DBD	C_{inorg}	C_{org}	$\delta^{13}C_{org}$	N	P
DBD		**−0.652*****	**−0.731*****	**−0.547*****	**−0.736*****	−0.049
C_{inorg}	< 0.001		0.117	**0.602*****	0.110	**−0.278***
C_{org}	< 0.001	0.358		0.146	**0.978*****	**0.427****
$\delta^{13}C_{org}$	< 0.001	< 0.001	0.263		.087	**−0.363****
N	< 0.001	0.388	< 0.001	0.505		**0.432****
P	0.717	0.026	< 0.001	0.004	< 0.001	

Pearson bivariate correlation coefficients are above the diagonal, with the significance of the correlation indicated below the diagonal. Correlation coefficients significantly different from zero are in bold type. Sample size (n) = 53 for comparisons involving $\delta^{13}C_{org}$, n = 56 for comparisons involving dry bulk density (DBD) and n = 64 for C_{inorg} (%), C_{org} (%), total N (%), and total P (%)

*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$

AGB (linear regression, $F = 9.32$, $p = 0.011$, $r^2 = 0.46$); AGB was a better predictor of soil C_{org} content than BGB ($F = 6.14$, $p = 0.031$, $r^2 = 0.36$), while leaf length was not a good predictor. Aboveground biomass was an even better predictor of soil density than C_{org} content; C_{org} density increased by 0.047 ± 0.013 mg C_{org} mL^{-1} of soil for every gram increase in biomass ($F = 13.4$, $p = 0.004$, $r^2 = 0.57$). Similar to our C_{org} content analyses, BGB was also a significant, but less powerful than AGB, linear predictor of C_{org} density, while leaf length was not.

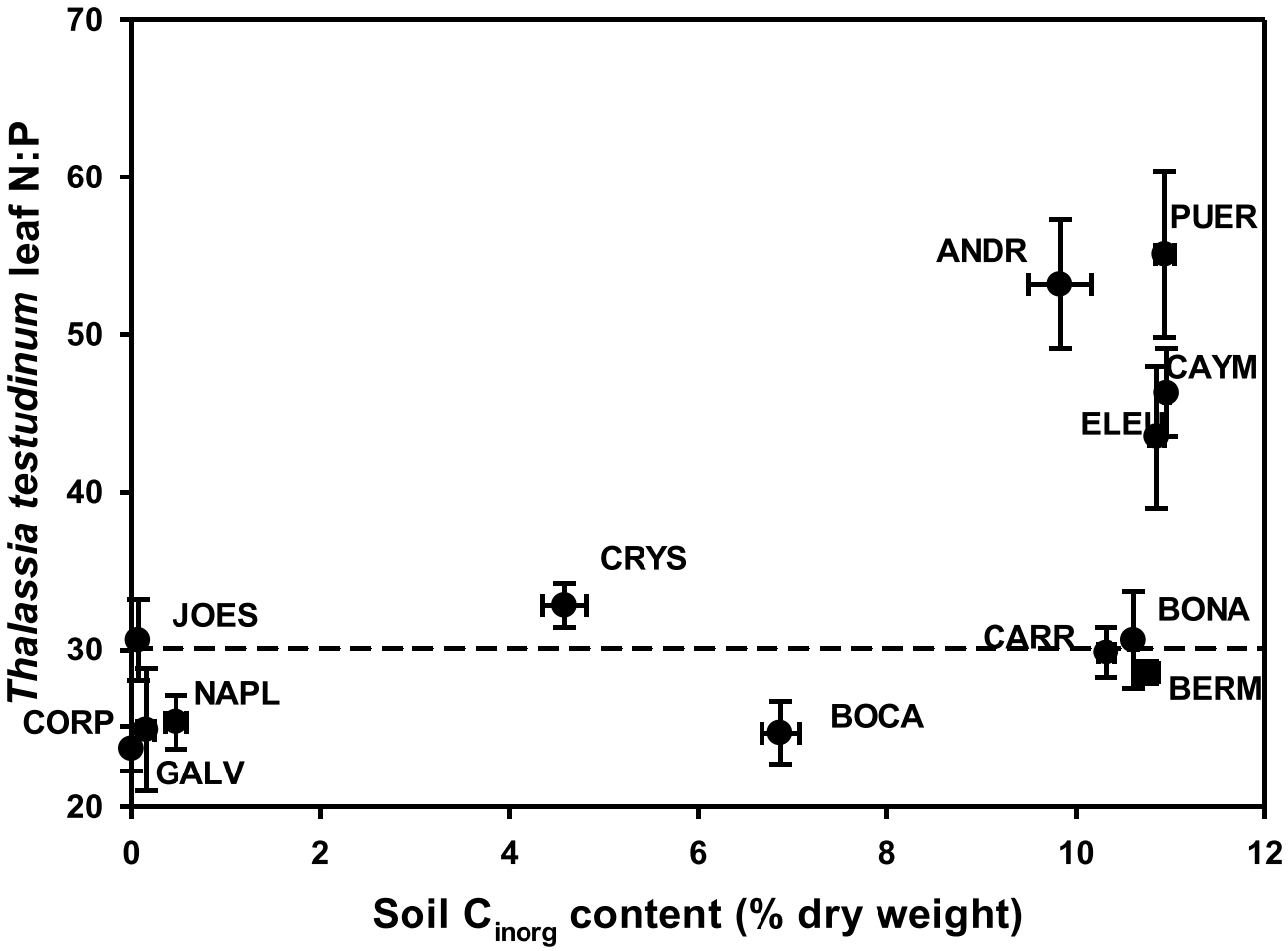

Fig. 6 Ratio of N:P of *Thalassia testudinum* leaves as a function of soil carbonate (C_{inorg}) content by site. The dashed horizontal line represents the 30:1 N:P ratio as in Fig. 5. See Fig. 4 caption for site abbreviations

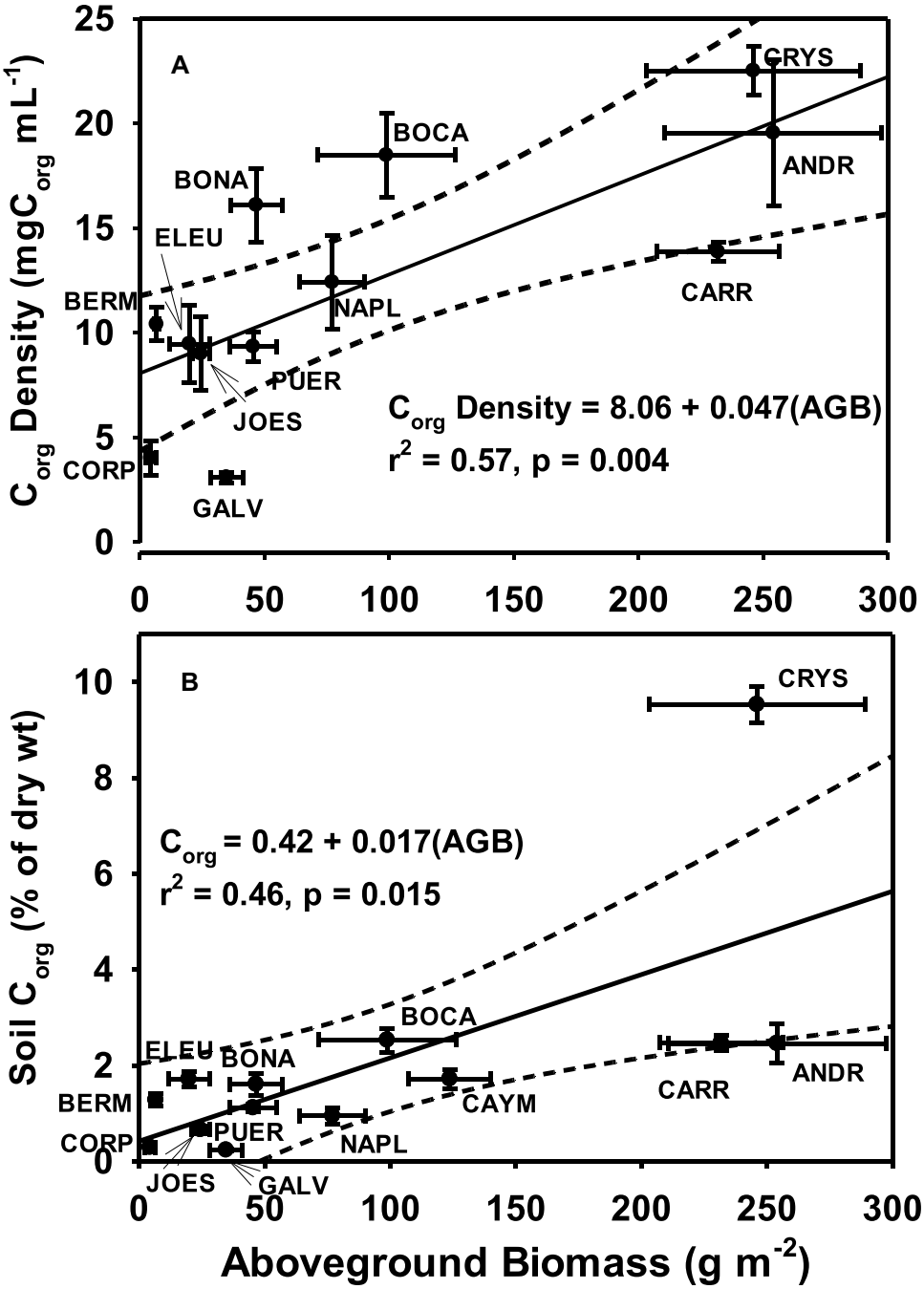

Fig. 7 **A** Soil C_{org} density as a function of seagrass abundance. **B** Soil C_{org} concentration as a function of seagrass abundance. Plotted values are site averages, with error bars representing ± 1 SE. Linear regressions with 95% confidence intervals. See Fig. 4 caption for site abbreviations

Stable Isotopes of Soil C_{org} as an Indicator of OM Provenance

The $\delta^{13}C$ and $\delta^{15}N$ of seagrass biomass varied greatly among sites (Fig. 8). $\delta^{13}C$ varied from a minimum of −13.1 ± 0.3‰ at Crystal River to a maximum of −5.9 ± 0.5‰ at Eleuthera. In general, $\delta^{13}C$ was lower for the sites located in the Gulf of Mexico than elsewhere. $\delta^{15}N$ varied from a low of −2.1 ± 1.0‰ to a high of 5.5 ± 0.9‰ in Bermuda. The higher latitude sites of Galveston, St. Joseph Bay, and Bermuda had the highest $\delta^{15}N$. These results indicate that seagrass-derived organic matter has site-specific stable isotope content that would be evident when it gets deposited on the soil surface.

Soil $\delta^{13}C_{org}$ was lower than the $\delta^{13}C$ of the overlying seagrasses (Fig. 8). Site-specific soil $\delta^{13}C_{org}$ ranged from −17.5 ± 0.2‰ at Galveston to −12.8 ± 0.5‰ at Andros. Because other putative sources for seagrass soil C_{org} are relatively depleted in ^{13}C compared to seagrasses, $\Delta^{13}C$ is a first indicator of the relative importance of seagrasses to the soil C_{org}. This metric indicated that seagrasses were a more important (lower $\Delta^{13}C$) contributor of C_{org} to the soils at sites like Bonaire, Andros, and Crystal River

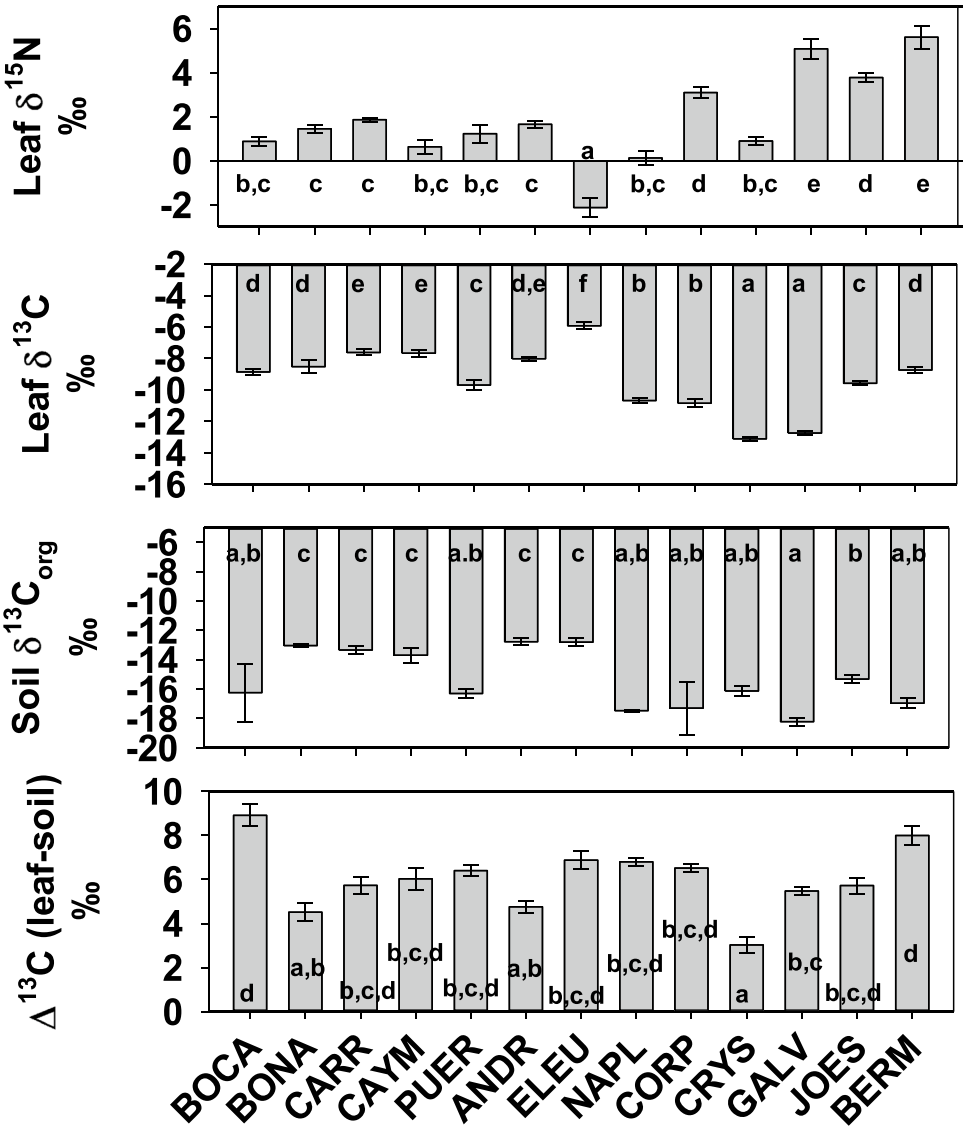

Fig. 8 Stable C and N isotope ratios for seagrass leaves and stable C isotope ratios and soil $\Delta^{13}C$ (the difference between site-averaged $\delta^{13}C$ of soil and seagrass leaves) by site, ordered by increasing latitude from left to right. Error bars indicate ± 1 SE. ANOVA indicated differences in means of all properties among sites ($p < 0.001$ for all comparisons), and letters designate homogenous subsets of sites for each soil property (S-N-K post hoc tests at $\alpha = 0.05$). Sites have been ordered by increasing latitude from left to right. See Fig. 4 for site abbreviations

compared to other sites like Bocas del Toro and Bermuda with higher $\Delta^{13}C$ (Fig. 8). Our mixing model results generally agreed with the $\Delta^{13}C$ but provided more nuanced results when considering the literature $\delta^{13}C$ values of terrestrial or phytoplankton C_{org} (Fig. 9). Overall, mixing models estimated seagrass to contribute the majority (51–76%) of C_{org} to sediments at all sites, except at Bocas del Toro and Corpus Christi, where seagrass contributions were predicted at 26% and 34%, respectively (Fig. 9). Sensitivity analysis, model estimates, and model diagnostics are shown in Supplemental Table S3.

Interrelationships Among Seagrass Abundance, Nutrients, and Soil Properties

Seagrass AGB was an informative predictor of the fraction of the soil C_{org} that was derived from seagrass biomass. $\Delta^{13}C$ decreased as AGB increased and the mixing model predictions of the importance of seagrass-derived C to the soil C_{org} increased as AGB increased (Fig. 10). Interestingly, neither seagrass BGB nor leaf length were informative predictors of the importance of seagrasses to soil C_{org} (linear regression, $p > 0.10$ in all cases).

Decomposition Rates of Standard Substrates Across Sites

Decomposition rates varied as a function of tea types and across sites. Averaging across all plots at all sites, green tea decomposed at a rate roughly 4 times faster than rooibos tea (paired sample *t*-test, k_g mean 1.27 ± 0.10% day^{-1}, k_r mean 0.27 ± 0.031% day^{-1}). Decay rate k_r varied among sites (Fig. 11, ANOVA, $F = 21.8$, $\alpha = 0.05$, $p < 0.001$), as did k_g (Fig. 11, ANOVA, $F = 23.8$, $\alpha = 0.05$, $p < 0.001$). However, site averaged k_g and k_r were closely and positively correlated with each other (Pearson's $r = 0.888$, $p < 0.001$).

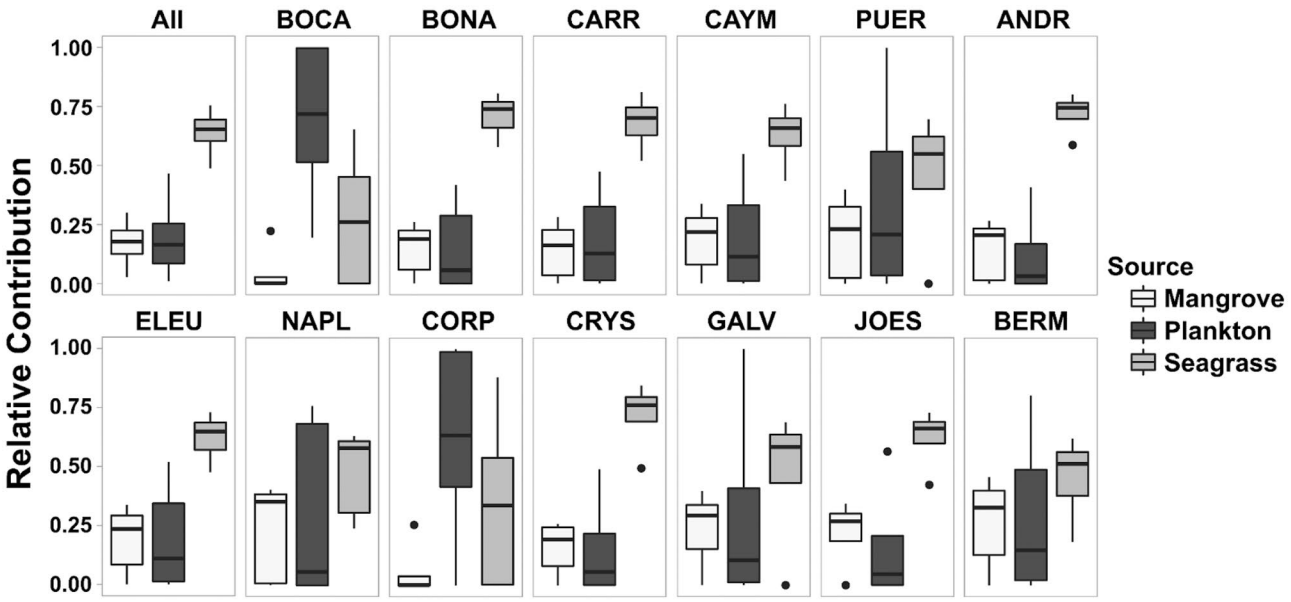

Fig. 9 Stable isotope mixing model results of fractional contribution of three putative organic matter sources (seagrass, mangrove-terrestrial, and phytoplankton OM). Boxes represent 25–75th percentiles of model results, horizontal bar within boxes show the median, whiskers represent 2.5–97.5th percentiles, and dots show outliers. Model result for "All" combine data from all sites into a single mixing model. See Fig. 4 for site abbreviations

While mean annual temperature differed among sites (Supplemental Fig. S3), temperatures varied little across sites during the tea bag decomposition assay (ranged from a low of 28.8 °C at St. Joseph Bay to 30.6 °C at Bocas del Toro) and were independent of site mean annual temperature or latitude. Hence, temperature differences at the times of the experiments did not explain the site-to-site variation in decomposition rates. As N availability relative to P increased, as indicated by *Thalassia testudinum* leaf tissue N:P, the rate of decay of the labile model substrate (k_g) increased, but there was no relationship detected between seagrass N:P and the decay rate of the more refractory model substrate (k_r) (Fig. 12). None of the other site-averaged soil or seagrass characteristics were correlated with decay rates of the standardized substrates.

Discussion

At the scale of the geographic range of this species in the Western Atlantic, we found that seagrass abundance was a good predictor of the C_{org} stocks in the surficial soils of *Thalassia testudinum* meadows and that the relative importance of seagrass-derived soil C_{org} increased as abundance increased. These patterns emerged regardless of differences in seagrass characteristics and soil properties, both of which varied greatly among our 13 sites. Seagrass abundance varied by more than an order of magnitude across sites. These relationships suggest that first-order estimates of surficial soil C_{org} stocks can be made by measuring seagrass abundance and applying a linear transfer function. Relative availability of the nutrients N and P to support plant growth was also correlated with soil C_{org} stocks. Stocks were lower at N-limited sites than at P-limited ones, but the importance of seagrass-derived organic matter to soil C_{org} stocks was not a function of nutrient limitation status. This finding seemed at odds with our observation that labile standard substrates decomposed more slowly at N-limited than at P-limited sites, since even though decomposition rates were lower at N-limited sites, less C_{org} was accumulating in the soils. The dependence of C_{org} stocks and decomposition rates on nutrient availability suggests that eutrophication is likely to exert a strong influence on carbon storage in seagrass meadows.

Variability in Soil Characteristics Across Sites

The C_{inorg} content, C_{org} content, and C_{org} density we observed covered almost the entire range documented for these quantities in the published literature for all seagrasses globally (Mazarrasa et al. 2015, and the associated published database). We found C_{inorg} values that were similar to the global distribution of C_{inorg} (range from 0.01 to 12.0%, $\bar{x} = 7.20 \pm 0.07\%$, and a median of 9.04%, $n = 3089$). It should be noted, however, that the global analysis of C_{inorg} is highly biased by data from carbonate terrains. When the global database was parsed to just the Western Atlantic and Caribbean ecoregion of our experiments, this bias toward

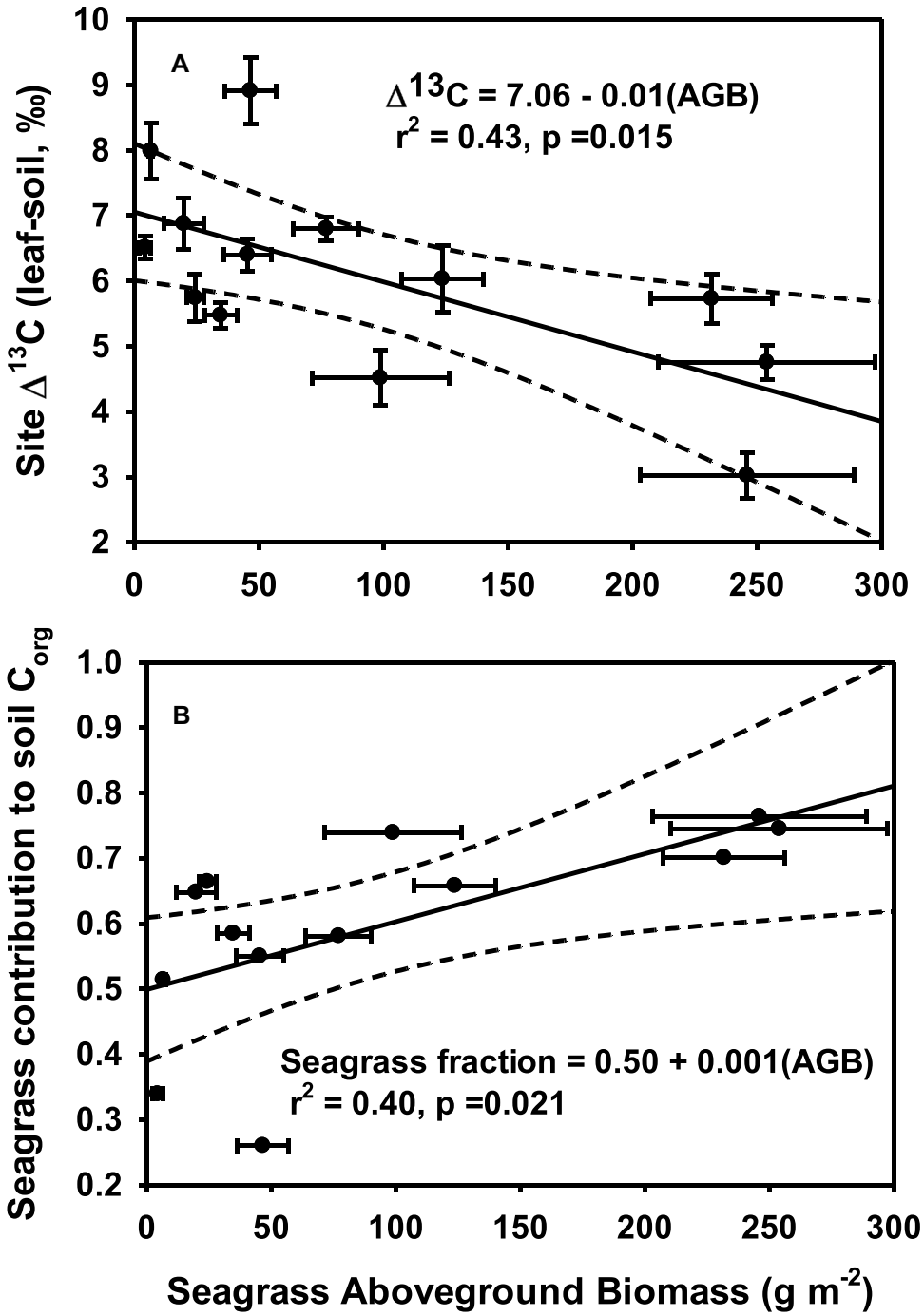

Fig. 10 **A** Soil $\Delta^{13}C$ (the difference between site-averaged $\delta^{13}C$ of soil and seagrass leaves) and **B** seagrass contribution (proportion estimated from stable isotope mixing models) as a function of seagrass aboveground biomass (g m^{-2}), by site. Plotted values are site averages, with error bars representing ± 1 SE. Linear regressions with 95% confidence intervals

high-carbonate sites persisted (C_{inorg} 0.18–11.69%, $\bar{x}$ = 9.87 ± 0.04, median = 10.07, n = 808). Our sampling helped overcome the bias in earlier data reported from the region, since we sampled four sites in low carbonate environments, seven from high carbonate environments, and two with a mixture of siliciclastic and carbonate sediments.

Worldwide, seagrass meadows dominated by *Thalassia testudinu*m are the third-ranked out of 25 seagrass species for the size of the C_{org} stocks they overlie (Kennedy et al. 2022). The C_{org} content of soils we sampled captured much of the reported range of C_{org} contents from all observations globally of C_{org} in seagrass beds of all species in the literature (Mazarrasa et al. 2015, and the supplemental database published for that paper). When the global data are restricted to the ecoregion of our study, C_{org} content ranged from 0.04 to 22.73% ($\bar{x}$ = 2.28 ± 0.07%, median = 2.02%, n = 808). While we had a wide geographical distribution of sample sites, we did not have a site representative of the highest soil C_{org} values found in seagrass meadows. Our 13 sites also displayed a range of C_{org} density on the low end of the distributions found either

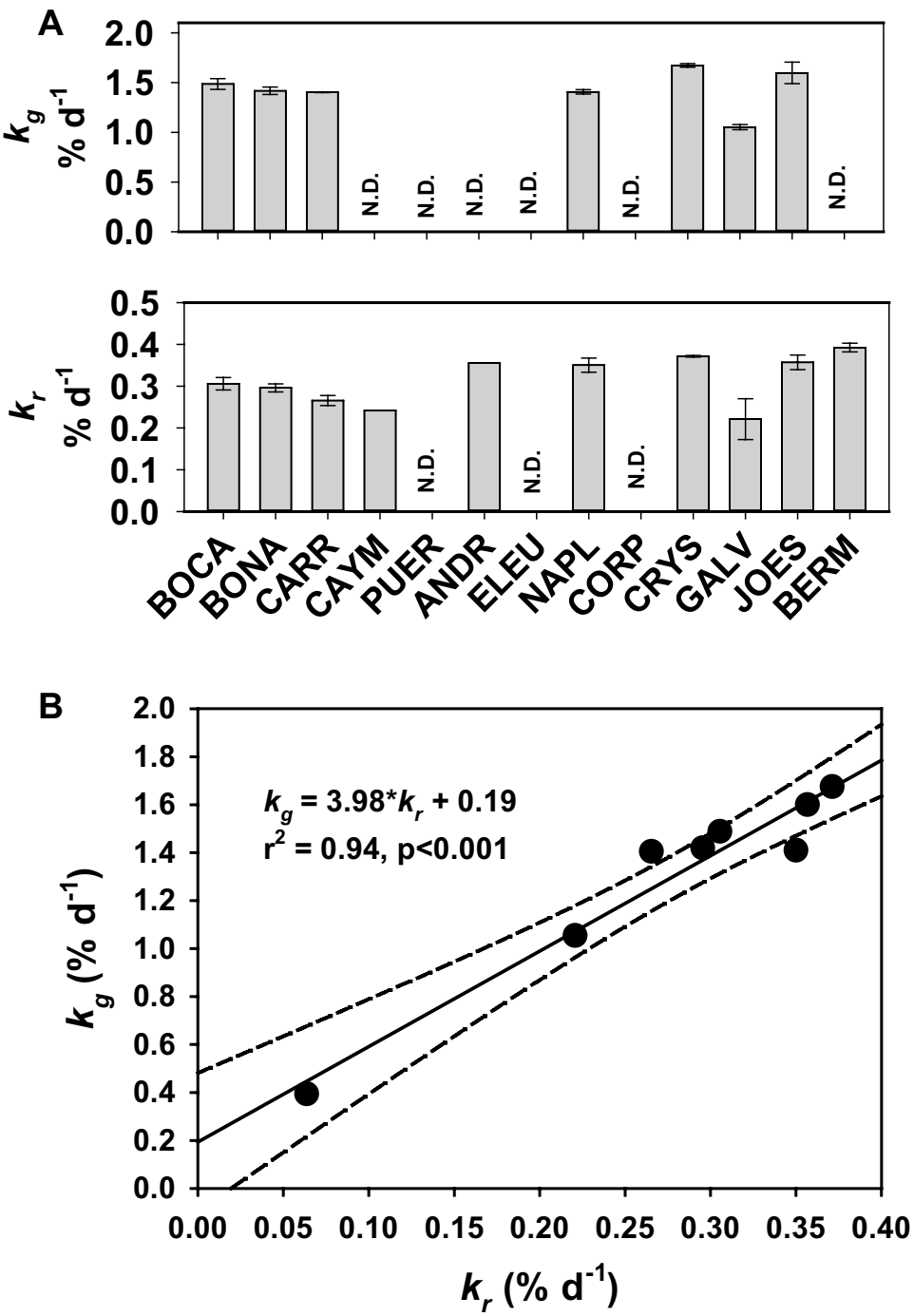

Fig. 11 **A** Decomposition rates of two model substrates, green (k_g) and rooibos tea (k_r), at the 13 study sites, ordered by increasing latitude from left to right. Error bars indicate ± 1 SE. ANOVA indicated differences in means of all properties among sites ($p < 0.001$ for all comparisons). **B** Linear relationship (linear regression) between k_g and k_r. Regression line is shown with 95% confidence interval

globally (0.01–160.16 mg C_{org} mL^{-1}, 13.74 ± 0.21 mg C_{org} mL^{-1}, median 11.84 mg C_{org} mL^{-1}, $n = 3076$) or in the ecoregion (0.44–91.4 mg C_{org} mL^{-1}, 17.83 ± 0.30 mg C_{org} mL^{-1}, median 17.23 mg C_{org} mL^{-1}, $n = 808$). Further, we added the high nutrient availability, high soil C_{org} Crystal River site to the diversity of site types that support *Thalassia testudinum*. While an outlier in our network, there are other such sites across the range of the species with similar characteristics (e.g., Barry et al. 2018; Carruthers et al. 2005). Possibly, our C_{org} stock data were lower than the global means because those previously reported global means are heavily biased by an overrepresentation of data from *Posidonia oceanica* meadows in the Mediterranean Sea, which are much higher than soil C_{org} stocks from other seagrass species (Kennedy et al. 2022).

We know of no similar global analysis of soil N and P content from seagrass meadows for comparison with our data, but our range of content are similar to the ranges observed in large data sets on seagrass soil P and N content from Shark Bay, Australia, and Florida Bay, USA (Fourqurean et al. 2012b).

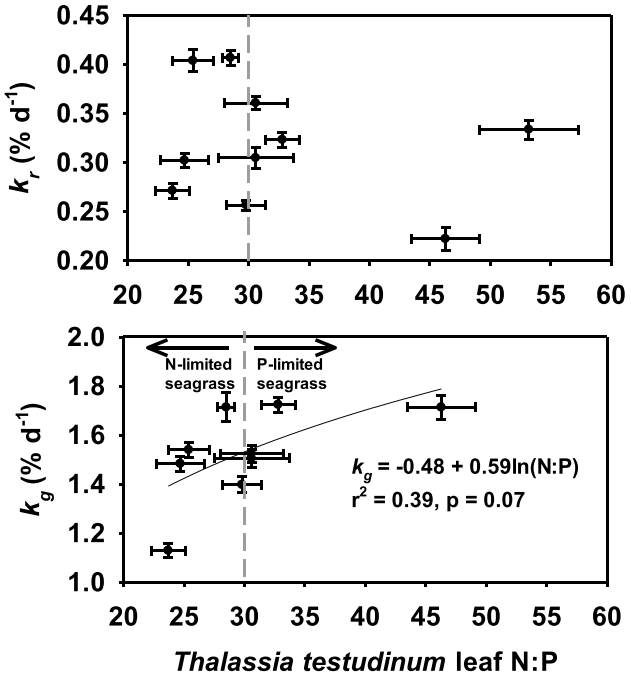

Fig. 12 Relationship between the rates of decomposition of rooibos tea (k_r), a refractory model substrate, and green tea (k_g), a more labile model substrate and the relative availability of N and P as indicated by the molar N:P of leaves of the dominant seagrass *Thalassia testudinum*. Each point represents the mean for one of our experimental sites, and error bars indicate ± 1 SE

Relationships Between Seagrass Abundance and Soil C_{org}

Both C_{org} content and density increased linearly as seagrass abundance increased. Abundance of seagrasses varied by over an order of magnitude across sites. Soil C_{org} content also varied over an order of magnitude among sites, but because of differences in soil dry bulk density among sites, C_{org} density varied by only a factor of 5. Other studies have found seagrass abundance to be a significant predictor of C_{org} (Greiner et al. 2013; Macreadie et al. 2015; Marba et al. 2015; Mazarrasa et al. 2015; Serrano et al. 2014), but at the landscape scale in south Florida, there is only a weak positive correlation between seagrass abundance and soil C_{org}, and sediment grain size is a much better predictor of C_{org} (Howard et al. 2021). In some landscapes, there is weak or no correlation between seagrass abundance and C_{org} (e.g., Barry et al. 2018; Campbell et al. 2015). Differences in findings across studies may have arisen due to differences in scale. Our results show that at the scale of the geographic range of *Thalassia testudinum*, estimates of seagrass C stores can be made by assuming a relationship between seagrass abundance and soil C_{org}. However, at this scale, almost half of the variance in soil C_{org} content was explained by other factors, suggesting further research is needed to improve estimates of soil carbon.

While AGB has to be deposited on the soil surface and buried in order to contribute to soil C_{org} stocks, BGB and any root OM exudates are added directly into the soils as plants grow and can thus contribute in a more direct pathway to the soil C_{org} stock upon decomposition. When species-specific plant morphological traits are compared with the average C_{org} stocks of meadows dominated by those species, BGB is a better predictor of C_{org} stocks than AGB (Kennedy et al. 2022), a conclusion largely driven by the inclusion of *Posidonia oceanica* that supports unusually large C_{org} stocks and also has much more biomass in belowground structures than other species. *Thalassia testudinum* has been documented to have the highest average BGB for any non-*Posidonia* seagrass species (supplemental information to Kennedy et al. 2022), but we found AGB to be a better predictor of C_{org} for *T. testudinum* in the Caribbean than BGB. Perhaps the relatively low value of BGB compared to AGB as a predictor of C_{org} we observed is owing to the very large variation in above- to belowground biomass ratios for *T. testudinum* (leaves can make up between 5 and 30% of total biomass of this species in a single embayment, Fourqurean and Zieman 1991). It is also feasible to estimate AGB from observational data without extensive excavation. Given that aboveground cover (as a fraction of the bottom obscured by the seagrasses) is closely correlated with AGB (Fourqurean et al. 2001), we suggest that remotely sensed or in-water estimates of cover can be used to generate a first-order estimate of C_{org} stocks.

Nature of Nutrient Limitation and Seagrass Abundance

The P content of seagrass soils was lower at carbonate sites characterized by high soil C_{inorg} (Table 1). In coastal marine systems, N limitation is common in temperate ecosystems with siliciclastic soils, whereas P limitation is often assumed to be restricted to tropical ecosystems with carbonate soils (reviewed by Howarth 1988; Short 1987). This generalization is largely attributed to biogeochemical sorption processes: strong P affinity to carbonate sediments results in a loss of phosphorus available for plant uptake. But our data show that rather than carbonates trapping and binding P making it unavailable to plants, carbonate environments actually sequester less P in soils. Not all tropical carbonate benthic ecosystems are P-limited (Erftemeijer et al. 1994; Ferdie and Fourqurean 2004; Udy et al. 1999), and our study provides further evidence for the decoupling of carbonate content and the identity of the limiting nutrient, suggesting there must be other factors that determine the limiting nutrient in some coastal marine ecosystems. In some systems, for example, P bound to soil C_{inorg} can be liberated and made available to seagrasses as organic matter exudates lead to

carbonate dissolution (Burdige et al. 2008). Indeed, not all our carbonate soil sites had seagrass N:P indicative of P limitation. High-carbonate sites like Andros, Puerto Morelos, the Cayman Islands, and Eleuthera had *T. testudinum* N:P clearly indicating P limitation, whereas N:P ratios in other high carbonate sites including Carrie Bow, Bonaire, and Bermuda indicated that some factor other than N or P was limiting seagrasses. And while the low carbonate sites Naples, Corpus Christi, and Galveston had *T. testudinum* N:P values clearly indicating N-limitation, the low-carbonate St. Joseph Bay site had N:P indicating neither N nor P limitation. Of the two sites of intermediate carbonate content, Bocas del Toro seagrass leaves showed a clear N-limitation signal while Crystal River had N:P close to the 30:1 ratio of balanced N and P supply. In addition, we found that C_{inorg} in seagrass soils was an imperfect predictor of the nature of nutrient limitation (as indicated by N:P ratio of plant leaves) for *Thalassia testudinum* across the sites (Fig. 6). We also found the highest soil C_{org} content at P-limited sites, which suggests that factors other than production of organic matter by seagrasses interact to allow for soil C_{org} accumulation. But because of the variability in plant N:P as a function of soil N and P content, soil C_{org} content increased as both soil N and P content increased (Table 1), suggesting that the processes leading to C_{org} and nutrient accumulation in seagrass meadows are similar while other site-specific factors control whether those soil N and P contents limit seagrass growth.

Interestingly, seagrass leaf N:P did not track soil N:P ratios at all sites. Bonaire, Crystal River, St. Joseph Bay, and Carrie Bow Cay had seagrass leaf N:P ratios near 30 while the soil N:P was higher (Fig. 5). As N:P near 30 is indicative of sufficient N and P availability to support plant growth, this would indicate that some other limiting factor, such as light or another resource, could be important at those sites.

Controls on Decomposition Rates

In addition to stimulating C_{org} production and the development of canopy architectures that could promote the settling of C_{org}, nutrients can stimulate microbial activity, and this microbial "priming" can mineralize otherwise stable stores of C_{org} in the soils (Carney et al. 2007; de Boer 2007; Deegan et al. 2012; Fontaine et al. 2003; Trevathan-Tackett et al. 2018). Indeed, P addition in very P-limited seagrasses can lead to decreases in soil C_{org} content (Armitage and Fourqurean 2016). We did find that, on a regional scale, the rates of decomposition of our labile standard organic substrate, but not our more recalcitrant standard substrate, were related to the availability of N to support seagrass growth, with a 55% higher decomposition rate at N-replete sites compared to N-poor sites.

Allochthonous vs. Autochthonous C_{org} in Seagrass Soils

The stable isotope mixing models suggest that seagrass material makes up a large share of the surficial sedimentary C_{org} pool across our study sites (Fig. 9), with larger seagrass biomass resulting in a greater proportion of seagrass-derived C_{org} in soil (Fig. 10). Our results speak only to the top 10 cm of seagrass soils. Since different organic matter sources have different lability (Enriquez et al. 1993), and seagrasses are largely composed of easily-degraded compounds (Trevathan-Tackett et al. 2018), older, C_{org} buried deeper in soils could be depleted in seagrass-derived C_{org}. The only sites where seagrass was not the main source of surficial sediment C_{org} were Bocas del Toro and Corpus Christi, where seagrass AGB and BGB were particularly low (Fig. 2). This low biomass would result in low production of seagrass C_{org} compared to denser seagrass sites.

Seagrass canopies are likely to increase trapping and deposition of all OM, not just the autochthonous OM produced within the bed (Hendriks et al. 2008); but particle settlement rates do not increase above a rather low canopy complexity threshold (Fonseca et al. 2019). As a consequence, increasing canopy complexity above that threshold is not likely to affect settlement of allochthonous and autochthonous organic matter nor change the relative importance of autochthonous C_{org} in the soils. Additionally, the majority of biomass (between 70 and 94%) of *Thalassia testudinum* is in belowground structures (Fourqurean and Zieman 1991), so it is likely that BGB production also contribute to the increase in soil C_{org} with increasing seagrass abundance and can therefore explain the increases in higher proportion of seagrass-derived C_{org} in soils from high-biomass sites. This mechanism likely also holds for the congener *Thalassia hemprichii* in the Indopacific since the range in $\Delta^{13}C$ values for *T. testudinum* in our study closely match the range reported for *T. hemprichii* (Kennedy et al. 2022).

Our stable isotope mixing models suggest that sites have a varied influence of terrestrial and planktonic organic matter to C_{org} that could be buried in the seagrass meadows. Interestingly, Bocas del Toro, adjacent to mountainous rainforest watersheds that produce very high runoff from the annual rainfall of > 3 m, and oceanic Bermuda with very little terrestrial runoff are at differing ends of the spectrum with respect to continental influence, yet at both sites, the seagrass contribution to soil OM is very low compared to other sites. Notably, these two sites also had very low seagrass abundance, suggesting that low rates of seagrass production were the dominant determinant of relative low rates of seagrass-derived organic matter in their soils rather than lack of allochthonous input.

Without site-specific information on stable C isotope signatures of plankton and mangrove/terrestrial sources,

and the relative abundances of those sources, our determinations of the relative importance of seagrass OM to the soils should be taken as preliminary. We know that some of our watersheds, especially those in the Gulf of Mexico, could be receiving terrestrial organic matter with a variety of sources and $\delta^{13}C$ values. One study found that ≥ 50% of the organic matter in continental shelf sediments in the northern Gulf of Mexico ultimately originated from C_4 plants like *Spartina alterniflora* and the grassland plants in associated watersheds (Goni et al. 1998) These C_4 plants have $\delta^{13}C$ values similar to seagrasses; our analyses did not include such plants as a possible contributor of OM to seagrass soils.

Limited Role of Temperature on Controlling Soil C_{org} at the Regional Scale

With the exception of the high soil nutrient and C_{org} at the Crystal River site, our higher-latitude, more seasonal, and therefore lower annual average temperature sites had low soil N and C_{org} content compared to more tropical sites. We did not find any patterns in decomposition rates of either labile or refractory standard organic matter substrates related to temperature, but we also intentionally measured decomposition rates during summer when there were not large differences in temperature across the sites. Given the well-known relationship between decomposition rates and temperature (Kirschbaum 1995), we expected that decomposition rates would be slower in cooler months at our high-latitude sites; however, high latitude sites are accumulating less C_{org} in their soils. This suggests that rates of primary production of *Thalassia testudinum*, a tropical plant, have greater control on soil C_{org} accumulation than differences in remineralization rates among sites.

Further Work Needed to Understand Factors Determining C_{org} in Soils

While our work suggests that seagrass abundance alone can, at the range of the distribution of the species, be used to produce first-order estimates of surficial C_{org} stocks, these relationships suggest that almost half of the C_{org} stocks are determined by factors other than seagrass abundance. Much work is needed to disentangle the other important drivers. The retention of C_{org} in seagrass soils relies on a depositional environment that is determined only in part by seagrasses (Miyajima et al. 2017). Other factors like the deposition and retention of C_{org} in seagrass soils are important in determining seagrass soil C_{org} stocks. Despite our finding good correlation at the scale of the range of the species, regional hydrodynamics interact with the spatial scale of nutrient addition to determine OM and nutrient content of seagrass soils at the landscape scale (Armitage and Fourqurean 2016; Howard et al. 2016). Consequently, soil C_{org} stores can be only weakly correlated with seagrass abundance at the landscape scale (Campbell et al. 2015; Howard et al. 2021). In tropical seagrasses, sites with low hydrodynamic energy are associated with areas of high soil C_{org} (Mazarrasa et al. 2021), but all our sites were selected in relatively low energy environments, and our site selection criteria restricted our sites to only relatively protected sites. Disturbance history may have just as important a role in determining C_{org} stores as present seagrass abundance. Carbon sequestration in the soil generally occurs on timescales of centuries to millennia (Callaway et al. 2012; Hansen and Nestlerode 2014), though stored carbon can be lost quickly if vegetation or soils are disturbed by natural (e.g., overgrazing, storm damage) or anthropogenic (e.g., dredging, water quality degradation) impacts (DeLaune and White 2012), particularly at large spatial scales (Macreadie et al. 2014). Understanding the fate of stored carbon lost because of disturbance is a critical need for understanding the roles that seagrasses play in the oceanic C cycle. Further, we only measured C_{org} content of the top 10 cm of the underlying soils. As soil C_{org} profiles vary with depth (Fourqurean et al. 2012a) and depth of accumulated sediments vary across the landscape, better estimates of seagrass C_{org} stocks call for more detailed analyses of entire soil profiles. Understanding how decomposition rates modify C_{org} in the soils after deposition is also much needed.

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Author Contribution JEC, AHA, JGD, KLH, VJP, JWF, and MJAC conceived and designed the experiments; JWF, JEC, OKR, CJM, AHA, JGD, KLH, VJP, ARA, SCB, EB, LRC, MJAC, GD, KD, TKF, BMG, RG, JAG, RGV, OAAK, STL, CWM, IGML, AMM, VAM, SAM, CMM, DAO, OO, LKR, ARR, LMRB, AS, YS, FOHS, US, JT, BIvT, WLW, and SSW performed the experiments and laboratory analyses; JWF, JEC, JRK, OKR, CJM, and CP analyzed and interpreted the data. JWF and JEC wrote the manuscript with contributions from the other authors.

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Data Availability Data used in this study will be available in the Figshare Data Repository.

Declarations

Competing Interests The authors declare no competing interests.

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