Carbon storage in seagrass soils: long-term nutrient history exceeds the effects of near-term nutrient enrichment

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Abstract

The carbon sequestration potential in coastal soils is linked to aboveground and belowground plant productivity and biomass, which in turn, is directly and indirectly influenced by nutrient input. We evaluated the influence of long-term and near-term nutrient input on aboveground and belowground carbon accumulation in seagrass beds, using a nutrient enrichment (nitrogen and phosphorus) experiment embedded within a naturally occurring, long-term gradient of phosphorus availability within Florida Bay (USA). We measured organic carbon stocks in soils and above- and belowground seagrass biomass after 17 months of experimental nutrient addition. At the nutrient-limited sites, phosphorus addition increased the carbon stock in aboveground seagrass biomass by more than 300%; belowground seagrass carbon stock increased by 50-100%. Soil carbon content slightly decreased (~10%) in response to phosphorus addition. There was a strong but non-linear relationship between soil carbon and *Thalassia testudinum* leaf nitrogen : phosphorus (N:P) or belowground seagrass carbon stock. When seagrass leaf N:P exceeded ~~a~~an approximate threshold of 75:1, or when belowground seagrass carbon stock was less than 100 g~~/m^2~~ m^{-2}, there was less than 3% organic carbon in the sediment. Despite the marked difference in soil carbon between phosphorus-limited and phosphorus-replete areas of Florida Bay, all areas of the bay had relatively high soil carbon stocks near or above the global median of 1.8% organic carbon. The relatively high carbon content in the soils indicates that seagrass beds have extremely high carbon storage potential, even in nutrient-limited areas with low biomass or productivity.

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1 Introduction

Increases in anthropogenic nutrient supply can alter coastal intertidal and subtidal plant communities by increasing aboveground biomass, lowering belowground biomass, or both (Deegan et al., 2012; Darby and Turner, 2008; Herbert and Fourqurean, 2009; Turner et al., 2009). Such changes in plant community structure are closely linked to the carbon storage potential of vegetated coastal ecosystems – a topic of key interest in emerging carbon markets (Russell et al., 2013; Couto et al., 2013; Alongi, 2014). Coastal ecosystems provide valuable "blue carbon" sequestration capacity, and may partially mitigate for or offset future climate change (Fourqurean et al., 2012a; Saintilan et al., 2013). However, plant biomass is a relatively labile carbon storage compartment – higher CO_2 concentrations may increase carbon storage in mangroves (Alongi, 2014) and seagrasses (Russell et al., 2013; Campbell and Fourqurean, 2013), but chronic nutrient enrichment may decrease it (Schmidt et al., 2012; Morris and Bradley, 1999). Therefore, recent attention has turned to the longer-term carbon storage compartment in the soil (Saintilan et al., 2013; Callaway et al., 2012).

Soil carbon is a large component of carbon storage in many coastal habitats (Donato et al., 2011; Chmura et al., 2003; Duarte et al., 2005; Mcleod et al., 2011; Armitage et al., 2011; Fourqurean et al., 2012a). The magnitude of soil carbon storage is linked to the mineral and physical characters of the soil (Rasmussen et al., 2007), with high carbon storage in soils with more clay (Schimel et al., 1994). Microbial communities are equally but inversely influential, with microbial decomposition and respiration generally causing net efflux of carbon from the soils in a process known as microbial priming (Schimel et al., 1994; Carney et al., 2007). The amount of organic carbon in the soil can be positively linked to aboveground and belowground plant productivity (Kirwan and Mudd, 2012). Seagrasses are highly productive, and have a particularly large storage capacity, relative to area (Fourqurean et al., 2012a). However, seagrass productivity is sensitive to nutrient (e.g., nitrogen or phosphorus) input, often decreasing substantially as a result of light limitation during macro- or microalgal blooms (Hauxwell et al., 2001; Schmidt et al., 2012; Burkholder et al., 2007). Therefore, near-term and long-term nutrient input may alter soil carbon storage potential in seagrass beds.

The quantity of carbon stored in coastal habitats is the net balance between inputs and losses. In nutrient-limited environments, nutrient addition increases primary productivity and biomass of plants, thereby increasing the rate of organic matter production, increasing trapping of allochthonous carbon, and preventing erosion of deposited carbon (Hemminga et al., 1991; Madsen et al., 2001; Gacia et al., 2002). Conversely, nutrients can stimulate microbial activity; this microbial priming can mineralize an otherwise recalcitrant pool of soil organic carbon (Carney et al., 2007; Fontaine et al., 2003). The net effect is likely to be context-dependent; the degree of nutrient limitation varies between sites and regions (De Boer, 2007), suggesting that the extent to which nutrients accelerate carbon loss may vary among sites.

Patterns of nutrient input to and availability in coastal systems can be driven by long-term, abiotic site conditions such as soil type or hydrology (Duarte, 1995; Fourqurean and Zieman, 2002; Short, 1987). Frequently, these mechanisms of nutrient supply and limitation are disrupted by near-term anthropogenic inputs (Orem et al., 1999; Tomasko et al., 2005). Carbon sequestration in the soil generally occurs on longer time scales (Callaway et al., 2012; Hansen and Nestlerode, 2014), though stored carbon can be lost quickly if vegetation or soils are disturbed by natural or anthropogenic impacts (DeLaune and White, 2012), particularly at large spatial scales (Macreadie et al., 2014). We evaluated the influence of long-term and near-term nutrient history on aboveground and belowground carbon accumulation in seagrass beds, using a nutrient enrichment experiment embedded within a naturally occurring, long-term gradient of nutrient availability within Florida Bay. In this system, P availability severely limits primary production in much of the eastern Bay (Fourqurean et al., 1992), and N limits some pelagic primary producers in the western Bay (Tomas et al., 1999). Our objectives were to (1) evaluate the effects of near-term nutrient addition on carbon storage in seagrass beds, and (2) determine if there was a relationship between soil carbon and seagrass nutrient limitation, as indicated by leaf nitrogen : phosphorus (N:P) ratios. In the P-limited Florida Bay ecosystem, low N:P ratios indicate higher availability of the limiting nutrient, P, and less severe long-term phosphorus limitation.

2 Methods

Our experimental design evaluated the ~~long~~near-term effects of nitrogen (N) and phosphorus (P) enrichment on above- and belowground carbon storage across a P-availability gradient. We used a three-way ANOVA design, where the factors were P addition, N addition, and site (Armitage et al., 2011). In September 2002 we established six study sites (all depths < 2 m) within Everglades National Park in Florida Bay (Fig. 1). Most sites were dominated by *Thalassia testudinum*; *Halodule wrightii* and *Syringodium filiforme* were found at some sites, particularly the westernmost site, Sprigger Bank (Fig. 1). The three eastern sites (Duck, South Nest, Bob Allen) occurred in an area of severe P limitation (Armitage et al., 2005; Fourqurean and Zieman, 2002). Two middle sites (Rabbit Key, Nine Mile Bank) occurred in a region of low to intermediate P limitation (Fourqurean and Zieman, 2002), and the westernmost site (Sprigger Bank) was located in a region that had a balanced N and P supply (Armitage et al., 2005). At each site we established a grid of 24 0.25-m^2 study plots spaced one meter apart. We randomly assigned treatments (control, nitrogen only [N], phosphorus only [P], both nitrogen and phosphorus [NP]) to six plots per site; fertilizer was added bimonthly from September 2002 through April 2006; loading rates and application protocols are described in Armitage et al. (2011).

In February 2004, soil cores (1 cm diameter, 5 cm deep) were collected from each plot, dried at 60°C, and homogenized for ~~nutrient~~carbon analyses. A separate set of cores (volume 5 mL each) was collected and weighed wet and dry in order to calculate bulk density as grams of dry soil per liter.

In April 2006, we used a circular core (15 cm diameter, 15 cm deep) to subsample seagrass biomass in each plot. Seagrasses were separated by species, and tissue was divided into aboveground (photosynthetic) and belowground tissue (rhizomes + roots + other non-photosynthetic tissue). Epiphytes were removed by gently scraping seagrass leaves with a razor blade. Cleaned seagrass tissues were dried at 60˚C and weighed to determine biomass. Biomass results were reported by Armitage et al. (2011), and were used here to calculate seagrass carbon stores in g C~~/m^2~~ m^{-2}.

We measured the organic carbon (C) content of the soils and C, N, and P content of above- and belowground seagrass tissue. Carbon and N contents were determined using a CHN analyzer (Fisons NA1500), which reports nutrients as a percent of dry weight. We used seagrass biomass (g~~/m^2~~ m^{-2}) and ~~carbon~~C content to calculate aboveground and belowground seagrass carbon stocks in g C~~/m^2~~ m^{-2}. Stocks for each species were summed to calculate total seagrass carbon stocks in each plot. ~~For soils, carbon~~ We applied the method described in Fourqurean et al. (2012b) to assess the organic carbon (OC) content ~~was determined before~~of our carbonate soils.

Briefly, total C content of the dry soil and of the residue remaining after ~~loss on~~ ignition at 500 °C for four hours~~, and then percent organic carbon content (% OC)~~ was measured using a CHN elemental analyzer; % OC was calculated as % TC_{dry} - (% C_{ash} *(dry weight of soil/dry weight of residue)). This technique has been found to work well in the carbonate soils of Florida Bay (Fourqurean et al., 2012b). Soil organic carbon content was calculated from the % OC and the bulk density, and was reported as g C~~/m^{2}in~~ m^{-2} in the top 15 cm of the soil. P contents were determined by a dry-oxidation, acid hydrolysis extraction followed by a colorimetric analysis of phosphate concentration of the extract (Fourqurean et al., 1992). Molar N:P ratios were calculated for aboveground tissue of the most common seagrass species, *Thalassia testudinum*.

The effect of near-term nutrient enrichment on carbon stores in aboveground seagrass tissue, belowground seagrass tissue, and soils were analyzed with three-way fixed factor ANOVA (P addition, N addition, and site) following verification of homoscedasticity with Levene's test. Data were square root transformed if necessary to conform to the assumptions of ANOVA.

To assess the influence of long-term nutrient history (as estimated by leaf N:P in control plots) on soil carbon content, we used curve fit regression analyses to identify the best fit relationships. Soil organic carbon content (% or g~~/m^2~~ m^{-2}) from control plots were the dependent variables in separate analyses, and *Thalassia* leaf N:P was the predictor variable. We focused on *Thalassia* tissue because it was the most common species and occurred in most study plots. *Thalassia* was absent from the westernmost site, Sprigger Bank, so that site was excluded from this analysis. In order to determine if soil carbon stock was linked to seagrass productivity, we repeated this analysis with aboveground and belowground seagrass carbon stores as the predictor variables. In the curve fit analyses, we fitted regression models of increasing complexity to each set of dependent and predictor variables, and accepted the model where the predictive power (R^2 value) was higher than simpler models, but where that predictive power did not increase at the next step in complexity.

3 Results

The total carbon stock in aboveground seagrass tissue, which is a function of seagrass biomass, was 3x to 10x higher in P-addition treatments, but only at the three most P-limited sites in eastern Florida Bay (Site*P $p < 0.001$; Table 1; Fig. 2a). The aboveground carbon store was 10-30% larger in many of the N addition plots (Fig. 2a). Although there was no significant site*N interaction (Table 1), the positive effects of N addition on the size of the aboveground carbon store appeared to be strongest at the three western sites that were not as severely P-limited (Fig. 2a).

As with aboveground seagrass tissue carbon, belowground seagrass tissue carbon, a function of belowground biomass, also varied with site and P addition (Site*P $p < 0.001$; Table 2), but the site-specific responses were variable. Phosphorus addition increased belowground seagrass carbon by 50-100%, but only at one of the severely P-limited sites (Bob Allen Keys; Fig. 2b). The belowground seagrass carbon store was up to 30% smaller in P-addition plots at two sites with more moderate P limitation, Rabbit Key Basin and Nine Mile Bank (Fig. 2b). There was no effect of N addition on belowground seagrass tissue carbon.

Soil organic carbon content, expressed in g~~/m^2~~ m^{-2}, varied with site, N-, and P-addition treatments (Table 3), but there were no consistent treatment responses across sites. Differences among sites were not linked to long-term nutrient history; the eastern-most and western-most sites had similar soil organic carbon content. The effects of N and P addition on soil organic

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carbon were generally small and variable, yielding a significant three-way interaction term (Table 3; Fig. 3a). However, when expressed as a percent of dry weight, soil organic carbon content was about 10% lower in P addition plots at some sites (Site*P $p = 0.011$; Table 4), especially the two sites with more moderate P limitation, Rabbit Key Basin and Nine Mile Bank (Fig. 3b). A similar response occurred at the easternmost site, Duck Key (Fig. 3b).

Curve fit analysis with *Thalassia* leaf N:P ratio as the predictor variable identified logarithmic regression as the best fit for both measures of soil organic carbon content. Soil carbon content (in g~~/m^2~~ m^{-2}) was significantly predicted by *Thalassia* leaf N:P ($p = 0.009$, $R^2 = 0.243$; Fig. 4a). Soil percent carbon content was also significantly predicted by *Thalassia* leaf N:P ($p < 0.001$, $R^2 = 0.593$). Soil percent carbon was markedly lower in the three eastern, phosphorus-limited sites than in the western sites (Fig. 4b). There appeared to be a threshold in the seagrass leaf N:P and soil carbon relationships: when seagrass leaf N:P exceeded 75:1, there was less than 3% organic carbon in the sediment (Fig. 4b).

Curve fit analysis with *Thalassia* above- and belowground carbon stocks as the predictor variables identified close relationships with both measures of soil organic carbon content. Soil carbon content (in g~~/m^2~~ m^{-2}) was significantly predicted by *Thalassia* aboveground carbon stock (linear, $p = 0.008$, $R^2 = 0.242$; Fig. 5a). Soil percent carbon content was also significantly predicted by *Thalassia* aboveground carbon stock (linear, $p < 0.001$, $R^2 = 0.716$; Fig. 5b). Soil carbon content (in g~~/m^2~~ m^{-2}) was significantly predicted by *Thalassia* belowground carbon stock (linear, $p < 0.001$, $R^2 = 0.419$; Fig. 6a). Soil percent carbon content was also significantly predicted by *Thalassia* belowground carbon stock (logarithmic, $p < 0.001$, $R^2 = 0.791$; Fig. 6b). There was ~~a~~an apparent threshold in the seagrass belowground carbon and soil carbon relationships: when seagrass belowground carbon stock was less than 100 g~~/m^2~~ m^{-2}, there was less than 3% organic carbon in the sediment (Fig. 6b).

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4 Discussion

Soil carbon in Florida Bay seagrass beds was closely related to belowground seagrass carbon stock and to landscape-scale nutrient limitation patterns. Both of these relationships functioned on large temporal and spatial scales, and near-term nutrient enrichment had a relatively small effect on soil carbon. *Thalassia* leaf N:P is an accurate indicator of long-term nutrient history (Fourqurean et al., 1992), and it was closely related to soil % carbon, and, to a lesser degree, absolute soil carbon stock. Patterns of nutrient limitation at this spatial scale are linked to landscape-scale biomass and the rate of organic matter production (Herbert and Fourqurean, 2009; Armitage et al., 2005). In more productive seagrass beds, higher biomass increases trapping of allochthonous carbon, and prevents the erosion of deposited carbon (Hemminga et al., 1991; Madsen et al., 2001; Gacia et al., 2002), further augmenting soil carbon storage. Further, since a substantial fraction of seagrass primary production is released from roots and rhizomes as dissolved organic carbon (DOC) (Kaldy et al., 2006), the supply of labile DOC to the sediments will be higher in dense seagrass meadows with greater belowground biomass, relative to sparser seagrass beds. This DOC supply could augment the % OC in soils underlying dense seagrass meadows, or could act as a primer for the decomposition of refractory organic compounds.

Soil characteristics such as grain size and mineral composition are important influences on carbon storage and limiting nutrient bioavailability, often shaping the long-term nutrient history of a site (McGlathery et al., 1994; Schimel et al., 1994; Rasmussen et al., 2007). There is generally greater net adsorption of organic matter onto finer grained soils with higher surface areas (Mayer, 1994). The low shear stress within seagrass beds is likely to augment the settlement and retention of these small particles. In seagrass beds with higher biomass, the depositional environment will facilitate the trapping of fine sediment, creating a feedback that further increases the C content of the soils. In fact, the physical effect of increased biomass on C deposition may be similar in magnitude to the increased C supply in higher productivity beds. In addition, phosphorus readily binds to carbonate sediments such as those in Florida Bay (Short et al., 1985; McGlathery et al., 1994), and P is efficiently retained in the sediments for decades following near-term P enrichment experiments (Herbert and Fourqurean, 2008). Therefore, the effects of near-term enrichment may persist long after a fertilization event (Fourqurean et al., 1995). The carbonate sediments in our study system likely played an important role in controlling seagrass productivity and subsequent belowground input to the soil carbon stock.

Soil carbon content is often closely linked to microbial priming activity, where higher microbial respiration and decomposition rates will accelerate carbon efflux from the soil (Waldrop et al., 2004; Kirwan and Blum, 2011; Cleveland and Townsend, 2006). In many ecosystems, priming is augmented in response to near-term nutrient enrichment, leading to a net loss of soil carbon (Schimel et al., 1994; Carney et al., 2007; Sayer et al., 2011). In our study, fertilization had relatively small effects on soil carbon stores. There was a small (~10%) decrease in absolute soil carbon content in response to phosphorus addition, but only at three of the sites – one in the eastern Bay, and two in the nutrient-replete western Bay. Priming effects on soil carbon are complex, and are not simply based on nutrient availability – competition among microorganisms also plays an important role (Fontaine et al., 2003). Alternatively, there may have been an offset between carbon gains from higher belowground productivity (Armitage et al., 2011) and carbon losses due to microbial priming, resulting in little to no net change in carbon storage.

There was a relatively small response of soil carbon to our near-term, small-scale nutrient enrichment treatments. Although there was an increase in above- and belowground biomass following phosphorus enrichment at the eastern bay sites (Armitage et al., 2011), the biomass accumulation was not sufficient to affect soil carbon at the time scale of our experiments. In the western bay, there was greater ambient phosphorus availability, and therefore more benthic productivity at large spatial scales (Armitage et al., 2011). In the eastern bay, only small plots received fertilizer and therefore had high biomass; surrounding areas had very low biomass. The deposition and retention of organic matter into seagrass beds is influenced by surrounding production (Gacia et al., 2002), suggesting that the effective retention of autochthonous or allochthonous organic carbon requires larger areas of high biomass. In restored seagrass beds, it may take more than ten years for soil carbon accumulation rates to reach levels comparable to established seagrass beds (Greiner et al., 2013). Our eastern, phosphorus-limited sites had little biomass at the start of the study (Armitage et al., 2005), comparable to a newly initiated restoration project. ~~It~~Therefore, it is likely that enrichment would have to continue for ~~a similarly long time period~~many years before responses in soil carbon stores could be detected. Although added phosphorus can be retained for decades in this system (Herbert and Fourqurean, 2008), the spatial scale of our enrichment treatments was small, relative to the landscape, and had low potential to trap allochthonous organic carbon (Armitage et al., 2011). Therefore, soil carbon sequestration and plant biomass responses to nutrient enrichment appear to act on very different spatial and temporal scales.

An important predictor of soil organic carbon content in our study was seagrass biomass, particularly belowground biomass. The link between plant productivity and soil carbon storage is well known in terrestrial and marine ecosystems (e.g., De Deyn et al., 2008; Mcleod et al., 2011; Kirwan and Mudd, 2012). Soil carbon storage potential can be particularly high in seagrass beds, relative to biomass and area (Fourqurean et al., 2012a). However, soil carbon content is not consistently related to seagrass biomass (Campbell et al., 2015), suggesting that seagrass productivity is not the sole predictor of soil carbon stores. In regions where ~~seagrass productivity~~soil carbon storage is not directly related to seagrass productivity, carbon capture is augmented by the entrapment of a substantial amount of particulate carbon (Mcleod et al., 2011) and slow decomposition rates in the soil (Duarte et al., 2013).

Plant productivity is linked to long-term nutrient history (e.g., Day et al., 2006; Herbert and Fourqurean, 2009~~; e.g., Day et al., 2006~~). Accordingly, we expected that plant productivity, and corresponding carbon storage, would be higher in our study sites with less severe phosphorus limitation. This prediction was borne out to some degree – the western sites had lower *Thalassia* leaf N:P ratios and higher soil carbon, but there was a nonlinear relationship between seagrass leaf N:P and soil carbon. When seagrass leaf N:P exceeded ~~a~~an approximate threshold of 75:1, suggesting severe phosphorus limitation (Armitage et al., 2005), there was less than 3% organic carbon in the sediment. Despite the marked difference in soil carbon between phosphorus-limited and phosphorus-replete areas of Florida Bay, all areas of the Bay had relatively high soil carbon stocks. The severely phosphorus-limited eastern Bay had soil carbon content near the global median of 1.8% soil organic carbon content (Fourqurean et al., 2012a). Soil carbon content in the nutrient-replete western Bay exceeded that of productive seagrass beds in many other coastal regions (Campbell et al., 2015; Duarte et al., 2005; Kennedy et al., 2010; Lavery et al., 2013).

The relatively high carbon content in the soils indicates that seagrass beds have extremely high carbon storage potential, even in nutrient-limited areas with low productivity.

5 Conclusions

Near-term fertilization had a relatively minor impact on soil C stores despite large increases in living biomass. Long-term nutrient history, which controls productivity in this landscape, was related to both biomass and soil C stocks. Higher biomass should result in more efficient trapping of fine particles and organic matter in the sediments, suggesting that there could be a physical effect of increased biomass that rivals the influence of increased productivity. Therefore, long-term changes in nutrient supply to oligotrophic coastal ecosystems could increase C storage, provided that enrichment does not ~~lead~~ cause plankton or algal blooms that lead to the loss of seagrasses.

Author contributions

A. A. and J. F. designed the experiments and A. A. carried them out and analyzed the data. A. A. prepared the manuscript with contributions from J. F.

Data availability

All data used in this study are included in this manuscript and associated supplemental material.

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Table 1: Results of 3-way ANOVA of site, nitrogen (N), and phosphorus (P) addition on the carbon stock in aboveground seagrass tissue.

	df	MS	F	P
Site	5	34.8	35.1	<0.001
N	1	9.6	9.7	0.002
P	1	46.5	47.0	<0.001
Site*N	5	1.1	1.1	0.358
Site*P	5	13.6	13.7	<0.001
N*P	1	<0.1	<0.1	0.836
Site*N*P	5	0.8	0.78	0.564
Error	99	1.0		

Table 2: Results of 3-way ANOVA of site, nitrogen (N), and phosphorus (P) addition on the carbon stock in belowground seagrass tissue.

	df	MS	F	P
Site	5	332.6	104.1	<0.001
N	1	1.8	0.6	0.449
P	1	<0.1	<0.1	0.903
Site*N	5	3.3	1.0	0.395
Site*P	5	26.8	8.4	<0.001
N*P	1	6.7	2.1	0.150
Site*N*P	5	3.4	1.1	0.387
Error	101	3.2		

Table 3: Results of 3-way ANOVA of site, nitrogen (N), and phosphorus (P) addition on total soil organic carbon content (g~~/m^2~~ m^{-2}).

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	df	MS	F	P
Site	5	$1.1*10^7$	43.7	<0.001
N	1	$1.3*10^5$	0.5	0.467
P	1	$3.7*10^5$	1.5	0.219
Site*N	5	$3.0*10^5$	1.2	0.292
Site*P	5	$6.0*10^5$	2.5	0.037
N*P	1	$5.6*10^4$	0.2	0.632
Site*N*P	5	$8.9*10^5$	3.7	0.004
Error	108	$2.4*10^5$		

Table 4: Results of 3-way ANOVA of site, nitrogen (N), and phosphorus (P) addition on percent organic carbon in the soil.

	df	MS	F	P
Site	5	108.4	4389.3	<0.001
N	1	0.6	2.3	0.135
P	1	1.7	6.7	0.011
Site*N	5	0.2	0.7	0.660
Site*P	5	0.8	3.1	0.011
N*P	1	<0.1	<0.1	0.872
Site*N*P	5	0.4	1.5	0.208
Error	108	0.2		

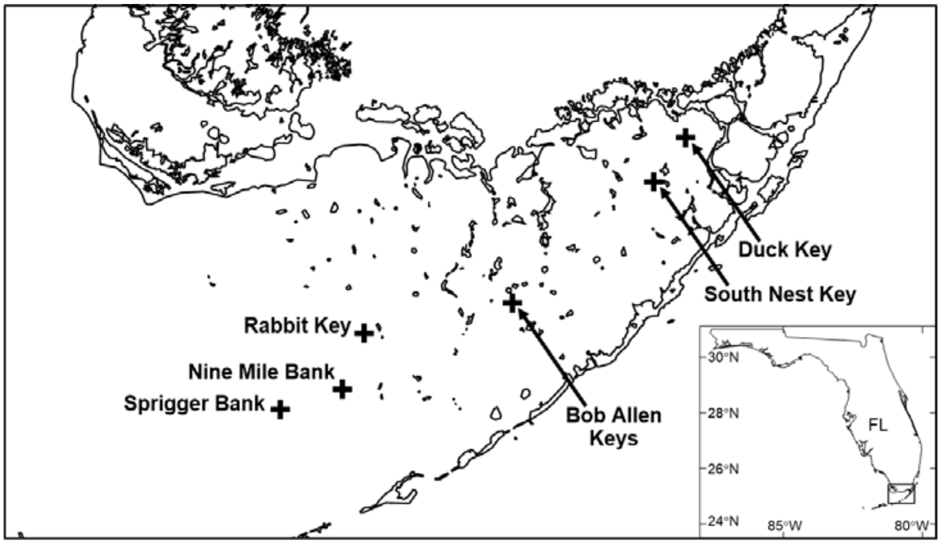

Figure 1: Map of Florida Bay and the study sites.

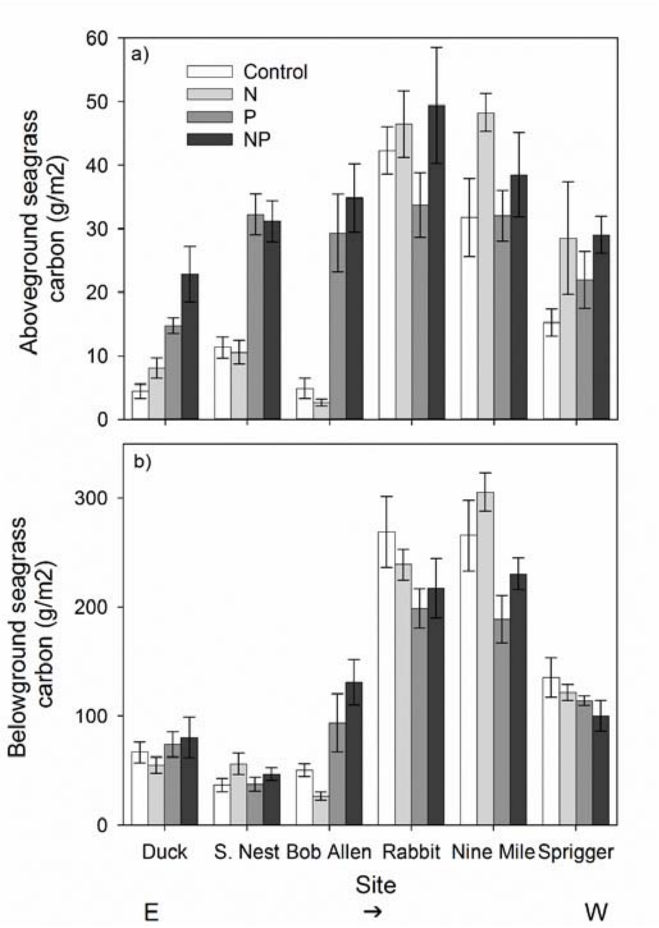

Figure 2: (a) Aboveground and (b) belowground seagrass carbon stocks at six sites in response to nitrogen (N) and phosphorus (P) addition. Sites are displayed along a naturally occurring P-availability gradient from low P availability in the east to high P availability in the west.

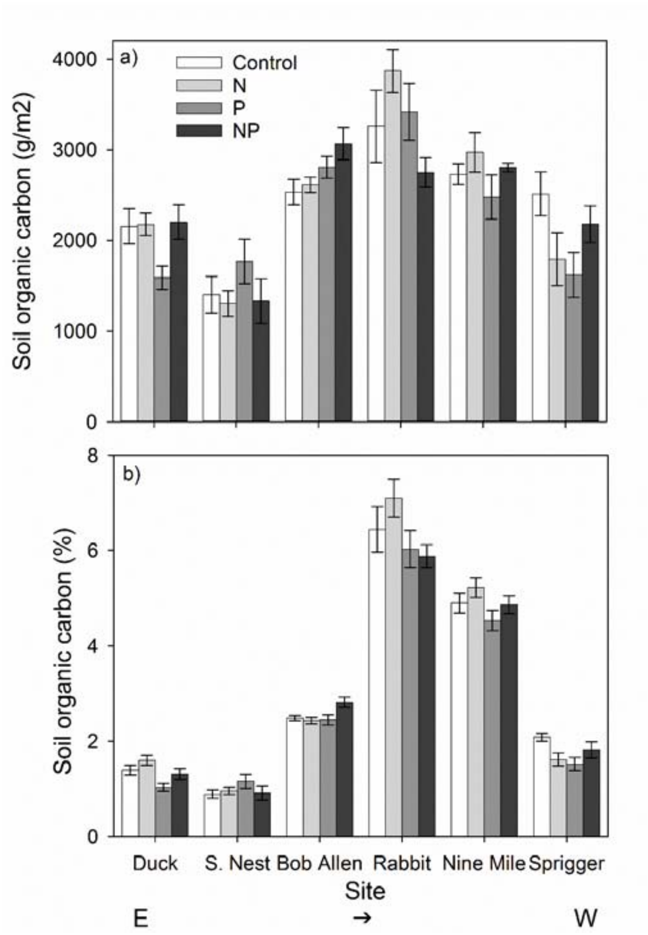

Figure 3: Soil organic carbon stocks, reported in (a) g~~/m^2~~ m^{-2} and (b) percent at six sites in response to nitrogen (N) and phosphorus (P) addition. Sites are displayed along a naturally occurring P-availability gradient from low P availability in the east to high P availability in the west.

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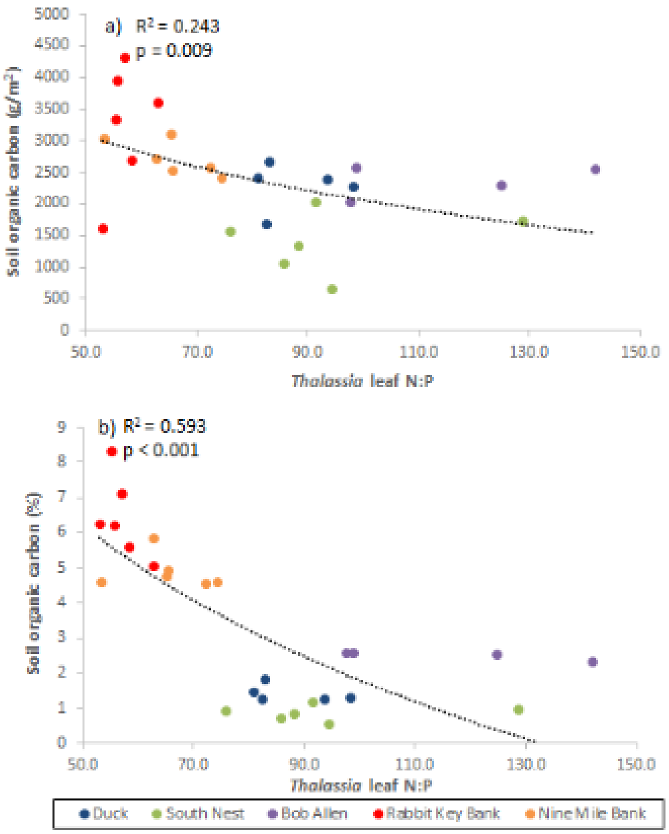

Figure 4: Logarithmic relationship between *Thalassia testudinum* leaf N:P ratio and soil carbon stock in control plots, reported in (a) g~~/m^2~~ m^{-2} and (b) percent. Sites are listed in the legend in order from east (most P limited) to west (least P limited).

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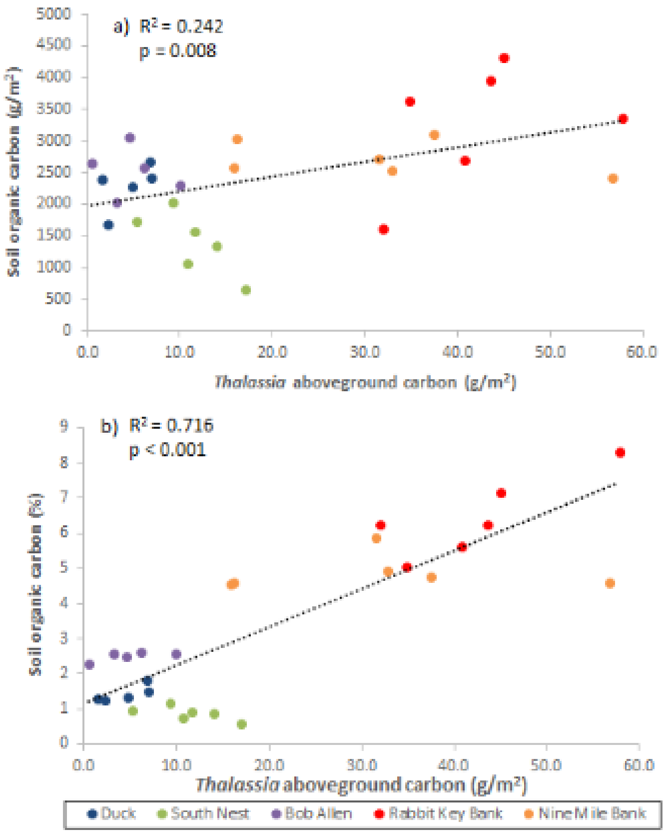

Figure 5: Linear relationship between *Thalassia testudinum* aboveground carbon stock and soil carbon stock in control plots, reported in (a) g~~/m^2~~ m^{-2} and (b) percent. Sites are listed in the legend in order from east (most P limited) to west (least P limited).

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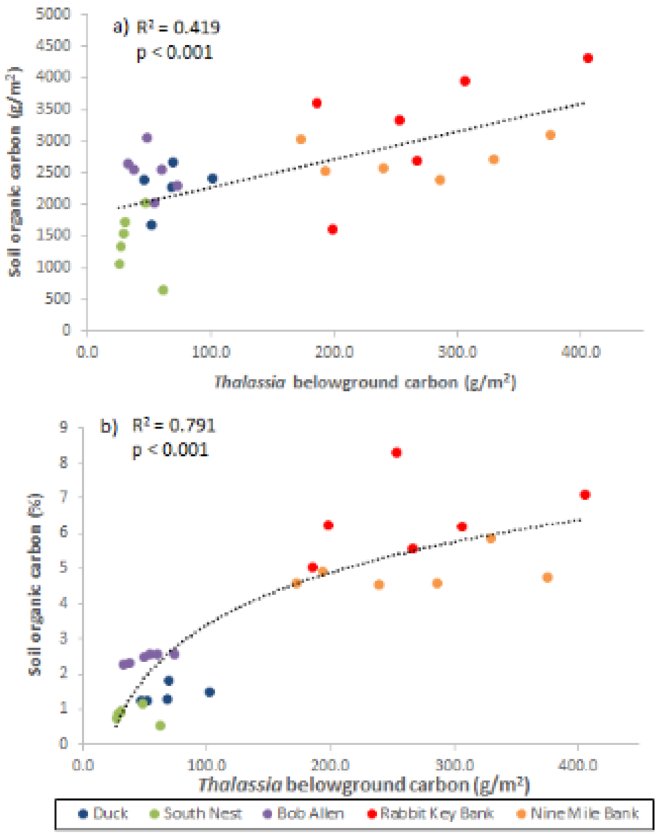

Figure 6: Relationship between *Thalassia testudinum* belowground carbon stock and soil carbon stock in control plots, reported in (a) g~~/m²~~ m^{-2} (linear) and (b) percent (logarithmic). Sites are listed in the legend in order from east (most P limited) to west (least P limited).

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