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ARTICLE

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Carbon dioxide fluxes and the dominant role of vegetation in recently created and reference Gulf Coast marshes

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Abstract

Coastal wetlands are one of the most productive ecosystems on Earth with the capacity to sequester large amounts of carbon dioxide (CO_2). Wetland loss due to anthropogenic and natural causes reduces the carbon (C) storage capacity and potentially releases previously fixed C in biomass and soil to the water column and atmosphere through decomposition. Coastal wetland restoration has the potential to mitigate some of the C losses depending on the balance of C fluxes. However, the role of vegetation and environmental conditions in governing rates of C accumulation in restoration sites is not well resolved. The purpose of this study was to examine seasonal C fluxes, specifically, gross ecosystem productivity (GEP), ecosystem respiration (ER), and net ecosystem exchange (NEE) of CO_2 in unvegetated and vegetated (*Spartina alterniflora*) areas of a 2-year old created marsh, and *S. alterniflora* and *Spartina patens* communities in a "natural" reference brackish marsh. *S. alterniflora*-dominated areas were sinks for CO_2 in both the newly created and reference marsh with an average CO_2 uptake rate of 7.0 $\pm$ 1.0 μmol m^{-2} s^{-1}. The unvegetated areas in the newly created marsh and *S. patens* areas in the reference marsh had approximately net neutral CO_2 fluxes. *S. alterniflora* areas of the created marsh had similar carbon fluxes to that in the reference marsh, despite a much lower soil organic matter content. Because vegetation develops much faster than soil properties, restored marshes can be a C sink equivalent to natural marshes as soon as the marsh is vegetated. Ecosystem productivity and C assimilation in *S. alterniflora* areas of the reference marsh were enhanced by lower elevations (up to 6 cm) and higher soil bulk density (up to 0.28 g cm^{-3}). At similar elevations, *S. alterniflora* in both the created and reference marshes was a greater C sink than *S. patens* areas of the reference marsh. Our findings illustrate that establishment of vegetation is critical to promoting C sink functions in created marshes and, notably, species do matter.

KEYWORDS
ecosystem respiration, elevation, gross ecosystem exchange, marsh plants, restoration, *Spartina alterniflora*, *Spartina patens*

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INTRODUCTION

Coastal saline marshes are important global carbon (C) sinks (Chmura et al., 2003; McLeod et al., 2011) as they are extremely productive (Odum, 1988), have relatively slow rates of decomposition and, unlike freshwater wetlands, have relatively low emissions of methane gas (Brevik & Homburg, 2004; Poffenbarger et al., 2011). Despite being important C sinks and providing numerous other ecosystem services, coastal marshes are vulnerable to loss from coastal development, hydrologic alterations, sea level rise, and other human impacts (Campbell et al., 2022; Day et al., 2000; McLeod et al., 2011; White et al., 2002). Marsh restoration and creation may offset some of the marsh area loss, though the potential for created marshes to function as similar C sinks to natural marshes is an area of active research and likely depends initially on the composition and productivity of the vegetation (Artigas et al., 2015; Cornell et al., 2007). The colonization and productivity of marsh plants in restoration sites are strongly dependent on the environmental conditions, which therefore also play a role in influencing C flux dynamics (Valach et al., 2021).

Wetland restoration sites have the potential to rapidly sequester CO_2 (Abbott et al., 2019; Burden et al., 2019; Cornell et al., 2007). Carbon fixation into newly created marshes begins with the colonization of edaphic algae and eventual colonization (or planting) of vegetation (Craft et al., 2003; Staver et al., 2020). A large proportion of this gross ecosystem productivity (GEP) is emitted back to the atmosphere through plant and algal respiration as well as microbial respiration via decomposition of soil organic matter (SOM), in total as ecosystem respiration (ER; Howes et al., 1985; Picek et al., 2007; Moseman-Valtierra et al., 2016; Yang et al., 2016). When GEP exceeds ER, the marsh functions as a CO_2 sink while when ER exceeds GEP, the marsh becomes a source of CO_2 to the atmosphere. Therefore, seasonality and environmental conditions affecting productivity and decomposition play a large role in the C balance of marshes. Natural marshes with large pools of SOM may have greater rates of ER through microbial respiration than newly created marshes. GEP may also differ among created and natural marshes due to greater competition for available resources and/or potential differences in environmental conditions such as elevation, nutrient availability, and soil properties (Valach et al., 2021). For example, created marshes can have similar C fluxes to those in natural marshes despite lower biomass of the same plant species due to greater productivity per unit biomass afforded by a higher leaf nitrogen content (Cornell et al., 2007). In this case, a higher leaf nitrogen content is indicative of greater soil nitrogen availability in the created marshes. Thus, restoration site conditions and designs have the potential to maximize marsh carbon sink potential making it important to empirically link C flux rates with environmental conditions.

Carbon fluxes and accumulation rates also tend to differ among plant species and vegetation zones (Artigas et al., 2015; Barry et al., 2022; Martin & Moseman-Valtierra, 2015; Moseman-Valtierra et al., 2016), which may have important implications for restoration site planning. In a natural marsh in New England, USA, the low marsh area dominated by *Spartina alterniflora* was a greater C sink than the high marsh-dominated *Spartina patens* (Moseman-Valtierra et al., 2016). In contrast, in a restored macrotidal marsh in New Jersey, the high marsh community consisting of planted *S. patens*, *Distichlis spicata*, and *Spartina cynosuroides* had greater CO_2 uptake than *S. alterniflora* planted in the low marsh (Artigas et al., 2015). While species differences have been found, species distribution is organized along gradients in elevation and hydrology making it difficult to isolate the effects of individual plant species. In a study that experimentally controlled for elevation, *S. alterniflora* was found to be a greater C sink than *S. patens* and *Phragmites australis* (Barry et al., 2023) indicating a strong species effect under similar environmental conditions.

The goal of this research was to test differences in CO_2 fluxes between created and natural marshes in representative vegetation zones, and to examine the role of environmental conditions such as marsh elevation, nitrogen availability and soil properties. Specifically, we compared CO_2 exchange (GEP, ER, andnet ecosystem exchange, NEE) between distinct habitats in a newly created marsh: (1) unvegetated sediments and (2) rapidly expanding *S. alterniflora* clones; and a "natural" reference marsh: (3) *S. alterniflora* and (4) *S. patens* communities. The habitats are representative of the communities present and allow three interesting lines of inquiry regarding C fluxes: (1) what is the influence of pioneer plants on C fluxes in a newly created marsh; (2) do C fluxes differ between created and reference marshes dominated by *S. alterniflora*; (3) do C fluxes differ between *S. alterniflora* and *S. patens* areas of a reference marsh; and (4) how do the measured abiotic factors influence these fluxes within and across habitats and marsh types? Vegetated areas of the created marsh were predicted to be a greater C sink than unvegetated sediments, associated with a greater GEP (Sheng et al., 2015; Figure 1). Rapidly expanding *S. alterniflora* in the newly created marsh was predicted to be a greater C sink than that in a natural reference marsh due to a lack of competition, higher photosynthetic rates, and greater utilization of nutrients resulting in greater productivity. Additionally, the created marsh was predicted to have lower rates of

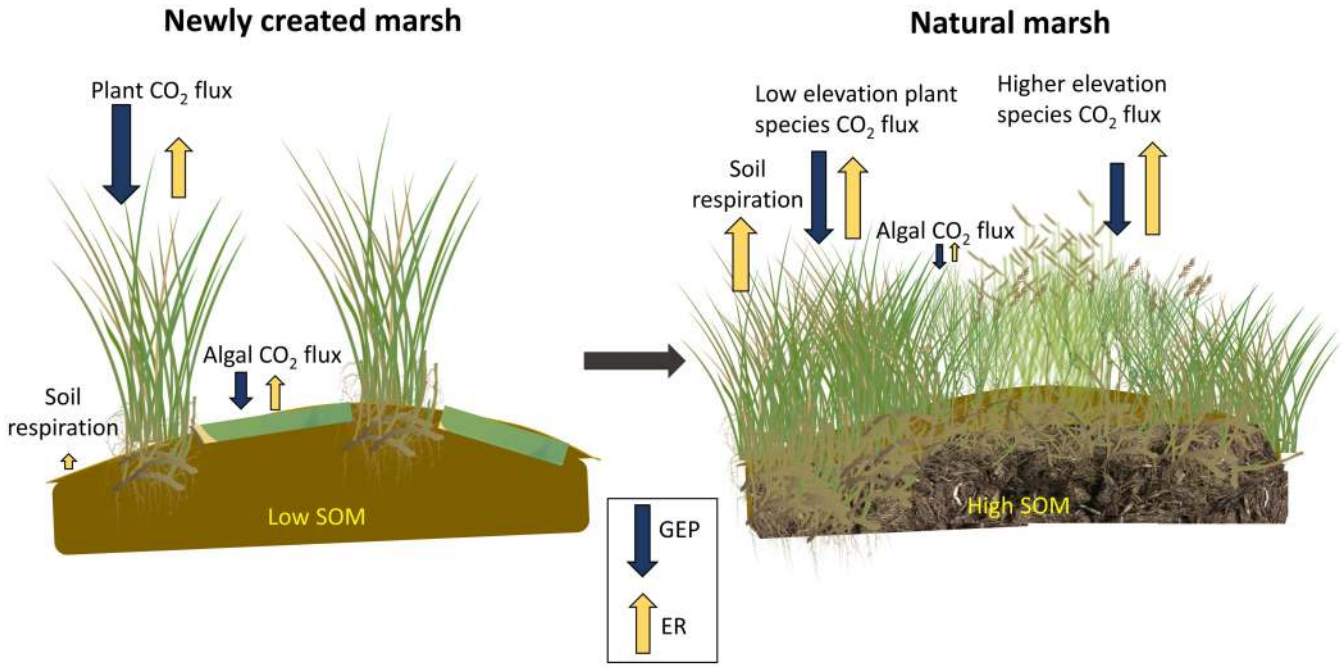


FIGURE 1 Hypothesized differences between ecosystem carbon fluxes due to differences in vegetation and soil between newly created and reference coastal marshes. The size of the arrows indicates the relative magnitude of the flux and net ecosystem exchange is the balance between gross ecosystem production (GEP), and ecosystem respiration (ER). Source of vector graphics: Tracey Saxby, Integration and Application Network (ian.umces.edu/media-library), University of Maryland, Center for Environmental Science, Integration and Application Network. SOM, soil organic matter.

ER than the natural marsh due to lower SOM content, less microbial biomass, and lower microbial activity (Abbott et al., 2022; Craft et al., 1999, 2003; Cornell et al., 2007; Edwards & Mills, 2005). *S. alterniflora* was also predicted to be a greater C sink than *S. patens* in the natural marsh (Moseman-Valtierra et al., 2016). Overall, vegetated areas of the created marsh were predicted to be a greater C sink than unvegetated areas in the created marsh as well as vegetated areas with the same species in the natural reference marsh. Species differences in C balance within the reference marsh were also predicted. Environmental factors including marsh elevation, soil nitrogen availability, SOM content, and bulk density were predicted to influence flux rates within and across habitats.

METHODS

Study site

The study was located in a large area of marshland between the Sabine and Calcasieu rivers in the Chenier Plain region of southwest Louisiana, USA (Figure 2A). The Chenier Plain occurs west of the Mississippi Deltaic Plain, and is characterized by distinct high elevation sandy-shell ridges exposed and consolidated by wave energy interspersed by low-lying marshland of fine-grained muds originally transported by longshore currents from westward distributary plumes of the Mississippi River (McBride et al., 2007). Historically, freshwater and low salinity wetlands dominated this area, but have widely deteriorated and converted to open water due to a combination of prolonged flooding and saltwater intrusion from past hurricanes, human alterations to hydrology within the system, and connection to the enlarged and deepened Calcasieu River Ship Channel (DeLaune et al., 1983; U.S. Fish and Wildlife, 2007, 2013). The study area is managed by the U.S. Fish and Wildlife Service Sabine National Wildlife Refuge (SNWR), who, in cooperation with the U.S. Army Corps of Engineers, has been implementing marsh creation projects for over 30 years. Over the last 100 years or so, salt-tolerant vegetation has colonized remnant marshes, which, in turn, serve as the source of natural colonization to nearby created marshes.

Marsh creation in this region involves pumping a slurry of sediment sourced from maintenance dredging of the Calcasieu ship channel into constructed containment dykes in areas that were historically marsh that have converted to open water (Inman, 2014). Vegetation succession in these created marshes has been well described (Abbott et al., 2019; Edwards & Proffitt, 2003;

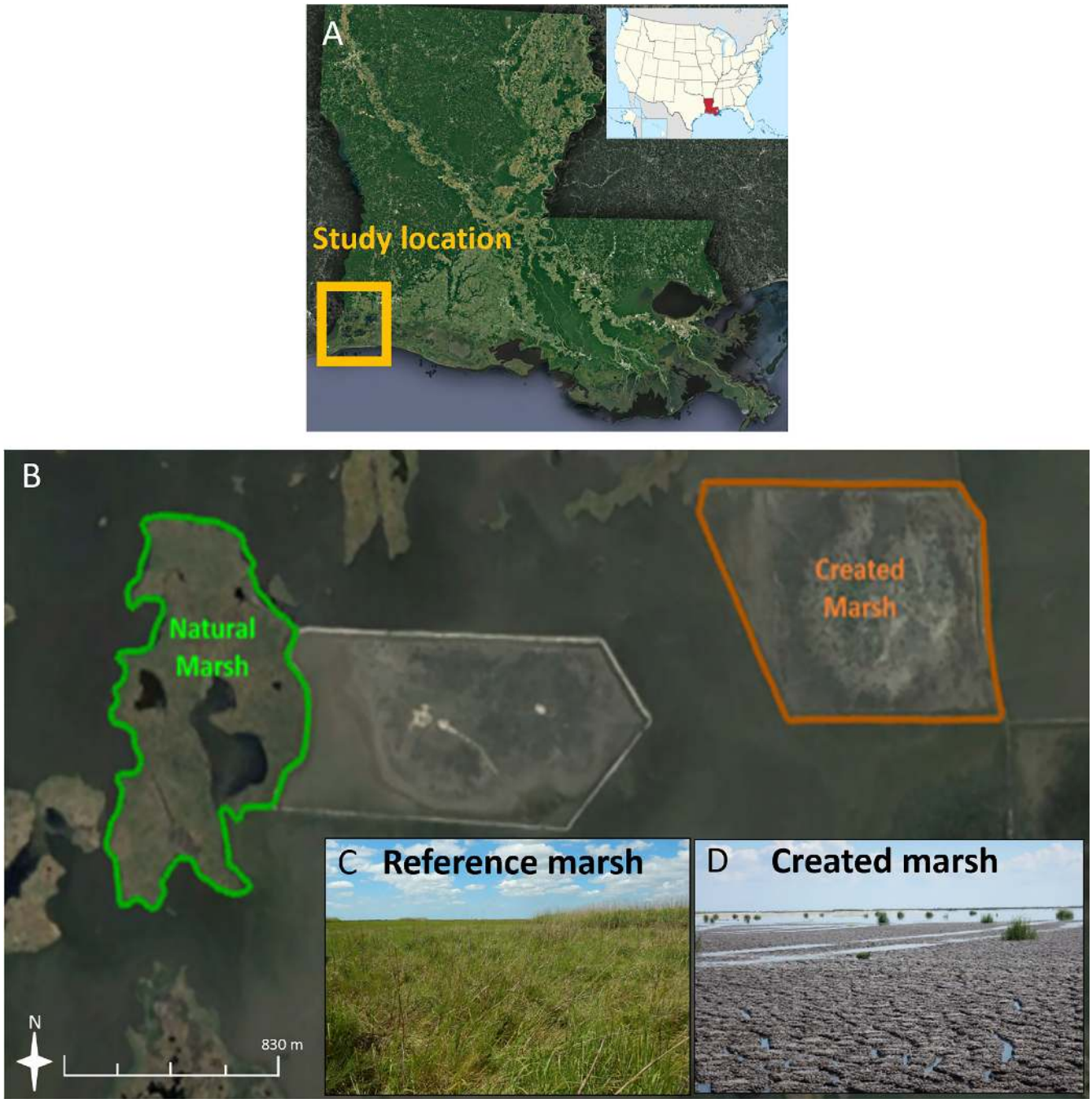


FIGURE 2 (A) Study locations in Sabine National Wildlife Refuge, Chenier Plain region, southwest Louisiana, USA; (B) satellite images of the natural reference and created marsh via Google Earth 2017; and pictures of the (C) natural reference and (D) created marshes. Photo credit: Andy Muench.

Muench & Elsey-Quirk, 2019; Owens et al., 2007; Proffitt et al., 2003, 2005). Typically, created marshes are initially colonized by clones of *S. alterniflora* along with other halophytic species such as *Salicornia bigelovii*. Within 3–5 years, the low marsh is dominated by *S. alterniflora* while mid-elevations are occupied by *S. patens* and *D. spicata*, and high elevations by *Iva frutescens* and other high marsh forbs (Owens et al., 2007; Proffitt et al., 2003).

For this study, we used a 2-year-old created marsh constructed in 2015 and a nearby "natural" reference marsh (Figure 2B). The reference marsh is representative of remnant brackish marshes in this system that have been subject to indirect human alterations to hydrology combined with natural changes to the system. The reference marsh was dominated by a mix of species with stands of both *S. alterniflora* and *S. patens* (Figure 2C). At

the time of the study in 2017, the 2-year-old created marsh had large unvegetated areas and sparse clones of *S. alterniflora*, which expanded over the study period (Figure 2D). Clone patches of *S. alterniflora* in the created marsh were heterogenous, varying in size and biomass (Figure 2D).

Both the reference and created marshes occur in an inland basin with limited connection to tidal influence. The hydrologic connectivity between the inland marsh basin and the Calcasieu Ship Channel is regulated by a water control structure via Hog Island Gully. The microtidal range at Calcasieu Pass averages 0.37 m (NOAA station 8768094). Within the study basin, the tidal signal is extremely muted as illustrated by nearby water level data at Louisiana Coastwide Reference Monitoring Station (CRMS) number 6301 (Appendix S1: Figure S1; CPRA, 2021). The hydrology of the study marshes is therefore largely influenced by wind- and precipitation-driven flooding rather than tides (Bernier et al., 2011), and is moderated by water management through tidal gates. Monthly water level and salinity data averaged across 13 years from 2008 to 2021 at CRMS station 6301 illustrate the strong and fairly consistent seasonal dynamics, which were captured by our seasonal C flux measurements (Figure 3).

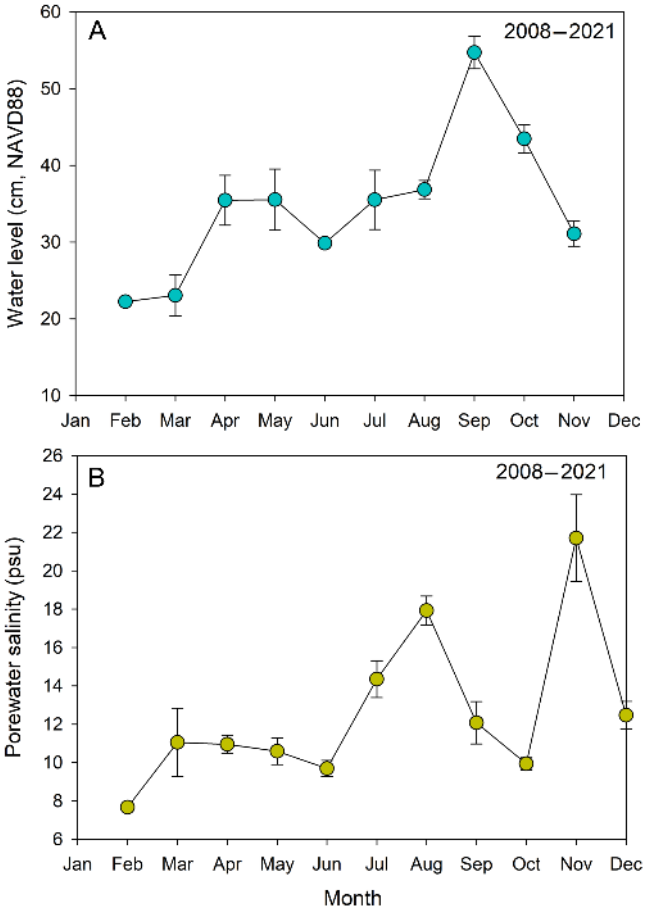


FIGURE 3 Monthly (A) water level and (B) salinity (means ± SE) collected from 2008 to 2021 adjacent to natural reference and created marsh study areas from the Louisiana Coastwide Reference Monitoring Station number 6301, Chenier Plain, Louisiana (CPRA, 2021).

Carbon fluxes

Four habitats were the focus of this study; two are representative of the created marsh: (1) unvegetated sediments, where algae and microphytobenthos may be dominant primary producers ("U"); and (2) newly colonized *S. alterniflora* clones ("Sa"); and two representative of the natural reference marsh: (3) *S. alterniflora* ("Sa"); and (4) *S. patens* ("Sp"). Carbon dioxide fluxes were measured in five replicate plots randomly located in each habitat type using the static chamber method ($n = 5$; Rolston, 1986; Lindau & DeLaune, 1991; Yu et al., 2013). Plots were at least 10 m apart. Gas chambers for the vegetated treatments consisted of a 30-cm^3 acrylic base unit placed to a depth 10 cm below the surface approximately one month prior to the first set of measurements. The base unit was left in place throughout the study. In May, July, and September 2017, one to three stackable 30 cm^3 acrylic chambers were assembled to accommodate the height of the tallest vegetation in each of the five plots per habitat. A base of one top unit was used for the non-vegetated plots in the created marsh. To ensure an air-tight seal, a water-filled collar surrounded the base of each stackable unit to limit external gas diffusion into the chamber. Carbon dioxide concentration was measured using an EGM-4 (PP Systems, Amesbury, MA) infrared gas analyzer to the nearest part per million at 1-min intervals for 10–20 min, or until the concentration was below the detection limit (~250 ppm). NEE was measured using transparent chambers while ER was measured using opaque chamber units. ER measurements were collected in the same plots following measurements of NEE and a 20 min equilibration period once opaque chambers were established to allow photosynthesis to cease.

NEE and ER have been found to vary with temperature and levels of photosynthetically active radiation (PAR) (Larcher, 2003; Neubauer et al., 2000). Therefore, temperature and PAR were measured along with CO_2 concentration using a probe attached to the EGM-4 (PP Systems, Amesbury, MA).

CO_2-flux calculations

NEE and ER were determined by linear regression of CO_2 change during the sampling interval where a strong

linear slope was present. The slope of that regression was used as either the NEE (clear chamber) or ER (opaque chamber; Appendix S1: Figure S2). The slope for NEE was taken only when full sunlight occurred in the sampling interval which is generally 1000 μmol m^{-2} s^{-1} or greater (Cornell et al., 2007).

The amount of CO_2 in the chamber at a given time was calculated as:

$$CO_2\ \mu mol = CO_2\ ppm/(22.4 \times (273 + C)/273) \times 27X.$$

The coefficient X is the number of chamber units stacked at each plot. Each chamber unit contains 27 L of air, and therefore X was multiplied by 27. The coefficient C is the temperature (in degrees Celsius) at the time of measurement. It should be noted that 22.4 is the molar volume of CO_2 at the pressure 1 ATM and 0°C. Our sites are at approximate sea level and, thus, are generally at 1 ATM pressure. Temperatures within the chambers were between 25 and 40°C and, therefore, temperature was corrected for in the above equation.

The GEP was calculated as:

$$GEP = -(NEE) + ER.$$

Negative GEP and NEE indicate gross and net C uptake, respectively. It was assumed that respiration rate during the dark incubations was equal to the respiration rate during daylight conditions, but this may not be the case as leaf respiration tends to increase under dark conditions (Atkin et al., 1997; Brooks & Farquhar, 1985; Kromer, 1995; Schulz, 2003).

Algal and plant biomass

To examine variation in algal biomass across treatments, sediment was collected adjacent to each gas exchange plot for chlorophyll *a* (chl *a*) analysis during each sampling in May, July, and September. Chl *a* content was determined from the top 2 cm of sediment by using sonication and 90% acetone (modified from Welschmeyer, 1994). Approximately 0.2 g of the sampled sediment was placed in 90% acetone, centrifuged at 5000×*g* for 5 min, and then sonicated. Following sonication for 30 s, the samples were placed in a freezer for one day and then centrifuged again at 5000×*g* for 5 min again the next day. Chl *a* content was then measured using a fluorometer (Turner Designs TD-700).

Aboveground biomass was estimated using allometry and measures of stem height and density measurements taken within the study plots in July and September 2017. The heights of up to 15 randomly chosen stems were collected in each plot. Stem density was determined by counting the number of stems within 0.09 m^2 for *S. alterniflora* and 0.01 m^2 for *S. patens*. To estimate the biomass of *S. alterniflora* in the reference marsh, the following equation was used for *S. alterniflora* in the region (Elsey-Quirk, unpublished data):

$$AB = -2032 + 521(\log\ height) + 136(\log\ density).$$

The equation used for *S. alterniflora* in the reference marsh was not used for *S. alterniflora* in the created marsh because the relationships between stem height, density, and biomass may differ due to different soil or nutrient conditions. For *S. alterniflora* in the created marsh and *S. patens* in the reference marsh, a coefficient relating height and density was derived from data in a previous study in the same marshes where stem height, stem density, and biomass were measured (Abbott et al., 2019). The coefficient was determined from the average biomass divided by the product of stem density and average stem height.

The equation used for *S. alterniflora* in the created marsh was:

$$AB = 0.0755(height)(density).$$

The equation used for *S. patens* in the reference marsh was:

$$AB = 0.0058(height)(density).$$

For all equations, height was measured in centimeters, density in stems per squre meter, and biomass in grams per square meter.

Environmental factors

Elevation relative to NAVD88 was measured at each plot using Leica Real Time Kinematic GS14. Three elevation readings were taken at each plot and then averaged. Horizontal and vertical accuracies of the measurements were 1 and 2 cm, respectively.

Sediment cores (7 cm diameter by 20 cm depth) were collected from each plot by hand in May 2017 using a plastic core barrel. Two depth intervals of 0–10 and 10–20 cm were sectioned and analyzed for bulk density, SOM content via loss on ignition (LOI), and soil nitrogen availability. Soil bulk density was measured for each depth section by drying to a constant weight at 60°C and dividing by the volume. A 1-g portion of the dried subsample was then combusted in a muffle furnace at 550°C for four hours. SOM was calculated by the proportion of sample lost on ignition.

Two measures of sediment nitrogen availability were made. Extractable ammonium (NH_4^+) was used to indicate the availability of nitrogen for primary producers in marsh sediment measured as milligrams of N per kilogram and potentially mineralizable nitrogen (PMN) was used to measure the rate at which extractable NH_4^+ increases with time in the sediment as an indicator of microbial-mediated ammonification (White & Reddy, 2000). For extractable NH_4^+, 5 g of homogenized sediment sample from each depth section of each core was placed into a 50-mL centrifuge tube with 20 mL of 2 M L^{-1} KCL. Tubes were placed into a horizontal shaker for one hour and then centrifuged at 5000×*g* for 10 min. Samples were filtered through 0.45 μm glass fiber filters into scintillation vials and preserved with H_2SO_4. Extractable NH_4^+ was determined using an AQ2 Automated Discrete Analyzer (Seal Analytical) via colorimetric analysis (USEPA, 1993).

PMN was determined by measuring extractable NH_4^+ at Days 0, 2, 5, and 10 of incubation under anerobic conditions (Roy & White, 2013). Day 0 was determined from initial extractable NH_4^+ concentrations from the soil samples. Three subsamples of each soil sample were homogenized, placed into glass serum bottles, which were evacuated and replaced with 99.99% N_2. The bottles were then injected with 20 mL of 10 psu salinity water purged by N_2 gas and placed into an incubator (IS-971R, Jeio Tech) at 40°C, continually oscillating at 100 rpm. The replicate serum bottles were removed at Days 2, 5, and 10 and extracted with 25 mL of 2 M L^{-1} KCl. Vials were placed into a horizontal shaker for one hour and then centrifuged at 5000×*g* for 10 min. Samples were filtered through 0.45-μm membrane filters into 20 mL scintillation vials and preserved with concentrated sulfuric acid to a pH < 2. Extractable NH_4^+ was determined using an AQ2 Automated Discrete Analyzer (Seal Analytical) for colorimetric analysis of the samples (USEPA, 1993). PMN was determined for each sample using linear regression of extractable NH_4^+ versus time.

Data analysis

Repeated measures ANOVA was used to test whether CO_2 fluxes (GEP, ER, and NEE) differed among habitats, seasons, and their interaction. We also tested differences among habitats within seasons using ANOVA. A two-way ANOVA was used to test for differences in elevation, aboveground biomass, and chl *a* concentration among habitats, and a mixed model was used to test differences in extractable NH_4^+, PMN, bulk density, and sediment organic matter content between habitats, depth, and their interaction using a repeated structure for depth. Regression analysis was used to examine the influence of chl *a*, extractable NH_4^+, PMN, soil bulk density, and organic matter content on CO_2 flux rates. All data were tested for normality, and log transformed as necessary. Data were analyzed using JMP SAS 13. For all of the statistical analysis, significance was determined by $\alpha = 0.05$.

RESULTS

Environmental conditions

Unvegetated plots in the created marsh averaged 6 cm lower than in the *S. patens* plots in the reference marsh ($p = 0.009$), but were similar in elevation to the *S. alterniflora* plots in the created and reference marshes. *S. patens* in the reference marsh was similar in elevation to that of *S. alterniflora* in both the reference and created marshes allowing a comparison between species in C fluxes unconfounded by differences in elevation and flooding dynamics (Table 1).

Water levels in the basin vary seasonally with relatively little variation from year to year (Figure 3A). Water level is typically 25 cm greater in September than during the spring and summer months, and lowest over the winter from November through March (Figure 3A). Thus, during our measurements, marshes were dry at the surface in May, moderately flooded (~10 cm depth) in July, and flooded completely to an approximate depth of 35 cm in September, generally reflecting the typical seasonal hydrologic patterns in the basin (Figure 3A). Salinity also varies seasonally with 7–12 psu typical in the early spring then increasing to a summer peak averaging 18 psu in August before declining to about 9 psu in October (Figure 3B).

Algal and plant biomass

Sediment chl *a* concentrations were greater in the reference marsh *S. alterniflora* areas than in all other habitats ($F_{3,59} = 9.40$, $p < 0.001$; Table 1). Chl *a* concentration was significantly lower in the *S. alterniflora* habitat in the created marsh than in the reference marsh ($p < 0.001$), despite similar aboveground biomass (Table 1) potentially due to differences in substrate characteristics. Aboveground biomass was similar across habitats ($p > 0.05$; Table 1).

Soil properties

Soil bulk density was approximately three times greater in the created marsh than in the reference marsh depending on depth (Figure 4A). For example, soil bulk

TABLE 1 Marsh elevation, aboveground plant biomass, and sediment chlorophyll *a* concentration in created and reference marsh habitats.

	Created marsh		Reference marsh	
Parameter	**Unvegetated**	***Spartina alterniflora***	***Spartina alterniflora***	***Spartina patens***
Marsh elevation (m, NAVD88)	0.104 ± 0.003^{B}	0.123 ± 0.005^{AB}	0.135 ± 0.005^{AB}	0.163 ± 0.008^{A}
Aboveground biomass (g m^{-2})	0	1026 ± 117	1054 ± 29	942 ± 76
Sediment chl *a* (mg kg^{-1} sediment)	465 ± 76^{B}	1626 ± 667^{B}	3969 ± 1081^{A}	827 ± 334^{B}

Note: Data are mean ± SE. Values within parameters sharing the same letters are not significantly different ($p > 0.05$).

density within the 10–20 cm depths was similar between the UC and SpR sites due to the wide variation in bulk density across the SpR areas. Across depths, the reference marsh had greater SOM content (28 ± 2%) than in the created marsh (10 ± 1%; Figure 4B).

The amount of extractable NH_4^+ at the 10–20 cm depth in the UC was significantly greater than in all vegetated habitats (Figure 4C). This indicates a large reservoir of available nitrogen ≥10 cm below the surface in the non-vegetated areas and suggests uptake and utilization of this available NH_4^+ by *S. alterniflora* in the created marsh. The upper 10 cm had similar concentrations of extractable NH_4^+ across habitats (Figure 4C). PMN rates were higher in the reference marsh *S. alterniflora* habitat than in the created marsh habitats and were similar between *S. patens* and *S. alterniflora* communities in the reference marsh (Figure 4D).

CO_2 fluxes

Overall, there was no seasonal change in GEP or NEE despite differences in timing during the growing season and marsh flooding ($p > 0.05$; Figure 5). Air temperature differed modestly across sampling dates ranging from 32°C in May to 39°C in July, and 37°C in September.

GEP differed among habitats within and across seasons ($p < 0.001$). In May, SpR had relatively low rates of GEP, similar to UC and lower than *S. alterniflora* habitats in both the created and reference marshes ($F_{3,14} = 10.6$, $p = 0.0007$; Figure 5A). In July and September, all vegetated habitats had similar rates of GEP, which were significantly greater than that of UC ($F_{3,16} = 14.2$, $p < 0.0001$; $F_{3,16} = 9.1$, $p = 0.0001$, respectively; Figure 5B,C). Averaged across seasons, GEP was greater in *S. alterniflora* in the reference marsh than unvegetated areas of the created marsh and *S. patens* habitat in the reference marsh ($F_{3,56} = 30.3$, $p < 0.0001$; Figure 5D).

ER also differed among habitats within and across seasons ($p < 0.001$). ER was significantly lower in unvegetated habitat than in all vegetated habitats in May and July, and only the reference marsh habitats in September ($p < 0.01$; Figure 5). Thus, in September, ER was similar between unvegetated and *S. alterniflora* areas of the created marsh. Averaged across the seasons, ER was 42 times lower in the UC (0.2 μmol s^{-1} m^{-2}) than in vegetated areas (8.5 μmol s^{-1} m^{-2}; $F_{11,45} = 6.8$, $p < 0.0001$).

NEE also differed among habitats with *S. alterniflora* in the created and reference marshes a greater C sink than in UC and SpR on average ($F_{3,47} = 7.4$, $p < 0.0001$; Figure 5D). NEE of SpR was very low similar to that of the UC (Figure 5D).

Factors influencing CO_2 fluxes

Marsh elevation had a major influence on CO_2 fluxes depending on habitat and season (Figure 6; Appendix S1: Figure S3). Across months sampled, *S. alterniflora* in the reference marsh was a greater C sink at lower elevations driven by greater GEP, whereas elevation had no effect on C fluxes in *S. patens* in the reference marsh (Habitat × Elevation: $R^2 = 0.28$, $p = 0.0404$; Figure 6). The strength of the relationship between NEE and elevation for *S. alterniflora* in the reference marsh was strongest in May and July, explaining over 75% of the variation during those months (Appendix S1: Figure S3C). However, in September, when the marsh was flooded, NEE was not related to elevation.

While C fluxes in the *S. patens* habitat in the reference marsh averaged across seasons did not vary with elevation, in May when GEP was low, elevation explained 98% of the variation with an increase in GEP at higher elevations (Appendix S1: Figure S3A). In July and September, there was no relationship between elevation and GEP in *S. patens* areas.

ER was positively related to elevation across habitats in September (but not May or July) mainly driven by low ER in the low elevation unvegetated sediments and high ER in the higher elevation areas of *S. patens* areas (Appendix S1: Figure S3B).

At similar elevations, all vegetated habitats had greater rates of GEP and ER than UC indicating the

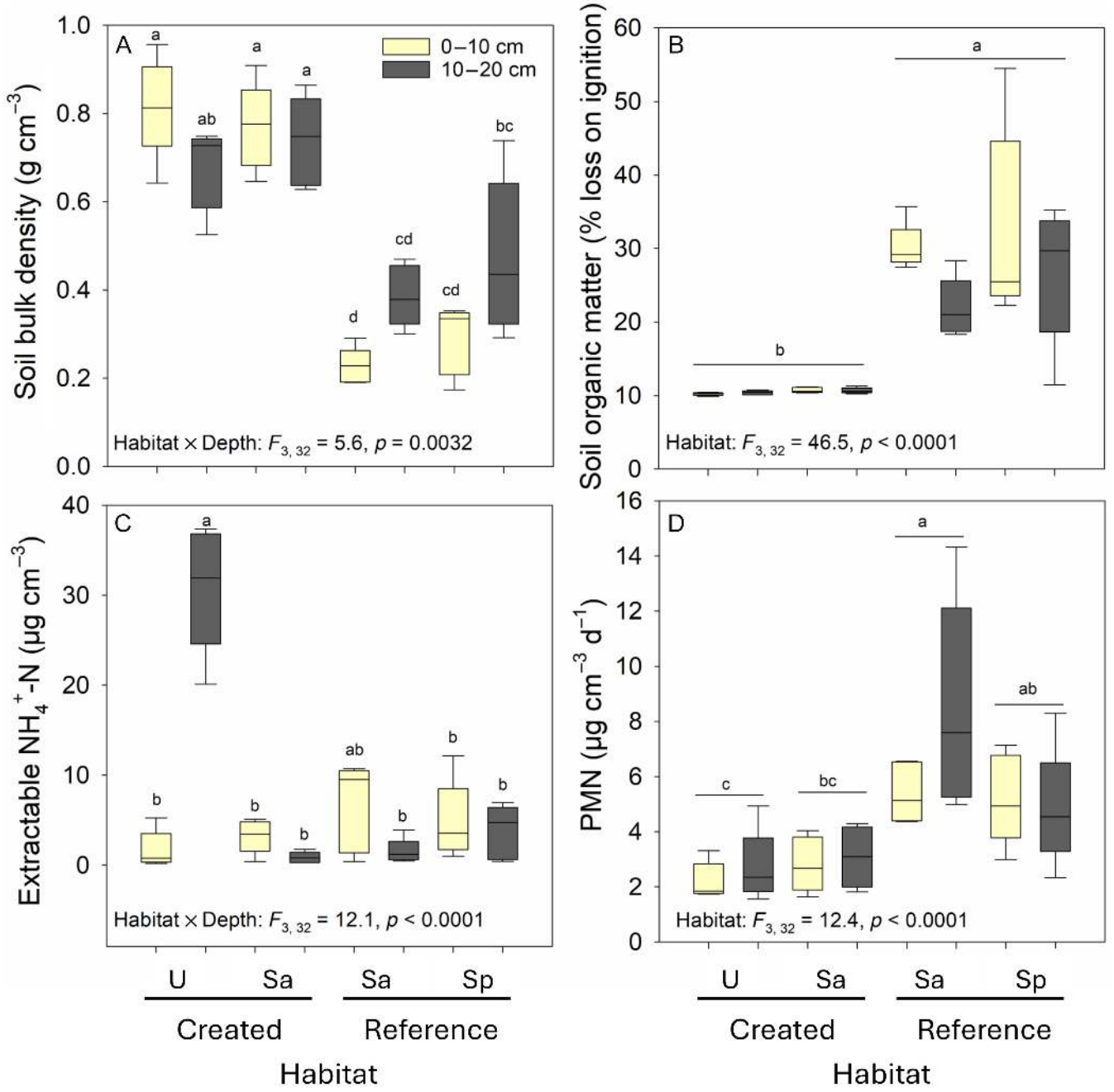


FIGURE 4 (A) Soil bulk density, (B) organic matter content, (C) extractable NH_4^+-N, and (D) potentially mineralizable N for depths of 0–10 cm and 10–20 cm in four habitat types: Unvegetated (U) and *Spartina alterniflora* (Sa) areas in a created marsh, and *Spartina alterniflora* (Sa) and *Spartina patens* (Sp) areas in a natural reference marsh in Sabine National Wildlife Refuge, Calcasieu, Louisiana. Boxplot interquartile range box represents the middle 50% of the data, the midline represents median values, and the whiskers the upper and lower 25% of the data. Different letters indicate significant differences within C flux and season ($p < 0.05$). Letters represent post hoc differences among habitats and depths. PMN, potentially mineralizable nitrogen.

significant influence of plants on CO_2 fluxes (Figure 6). Further, *S. alterniflora* in both the created and reference marshes was a greater C sink than *S. patens* in the reference marsh at similar elevations due almost entirely to greater rates of GEP (Figure 6). ER was generally similar among vegetated habitats at similar elevations.

Rates of GEP and ER were also positively related to aboveground plant biomass across habitats but the relationships were particularly strong within the created marsh *S. alterniflora* areas (Figure 7). The impact of biomass on NEE was negligible because higher rates of GEP were countered by higher rates of ER as biomass

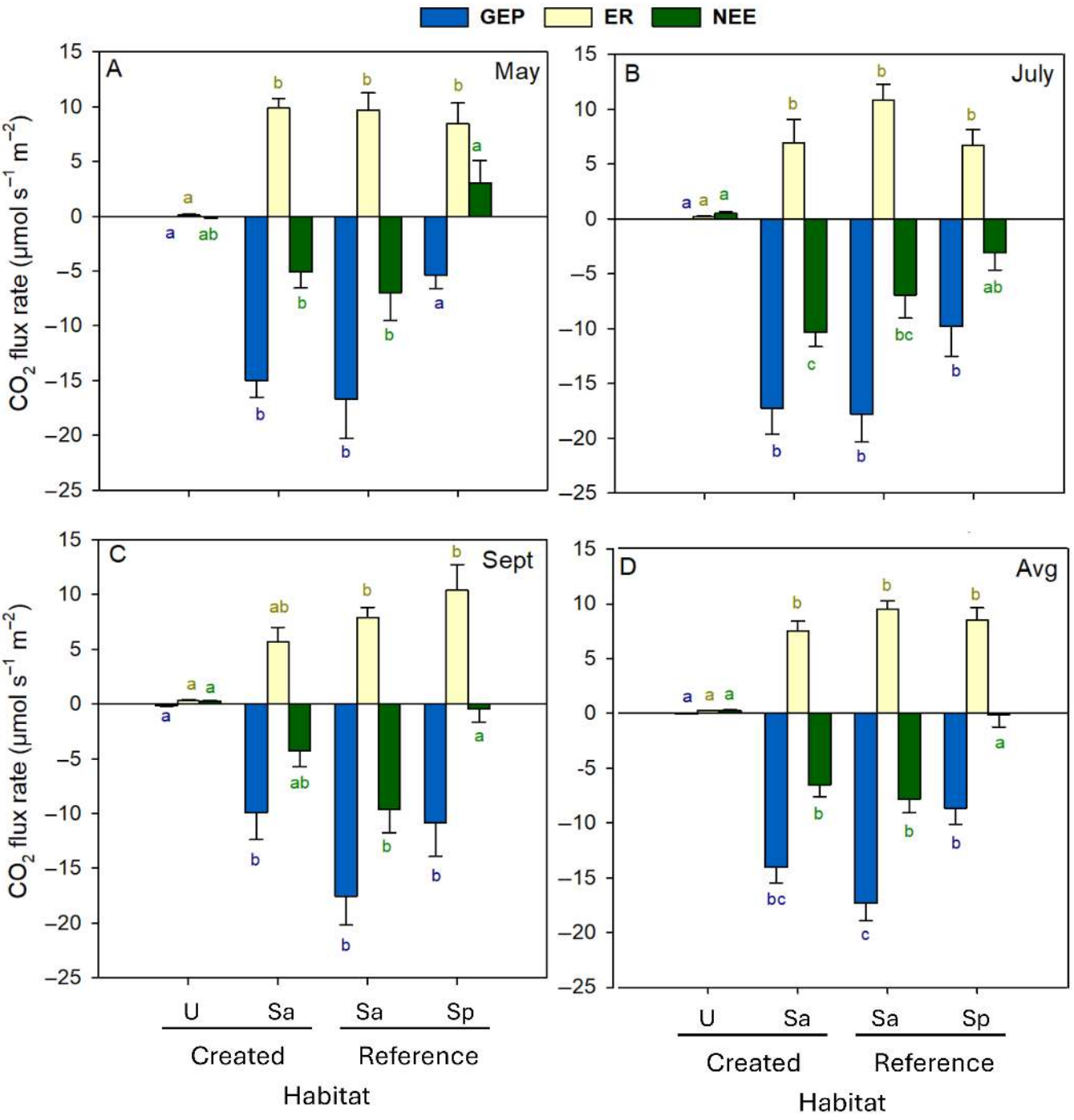
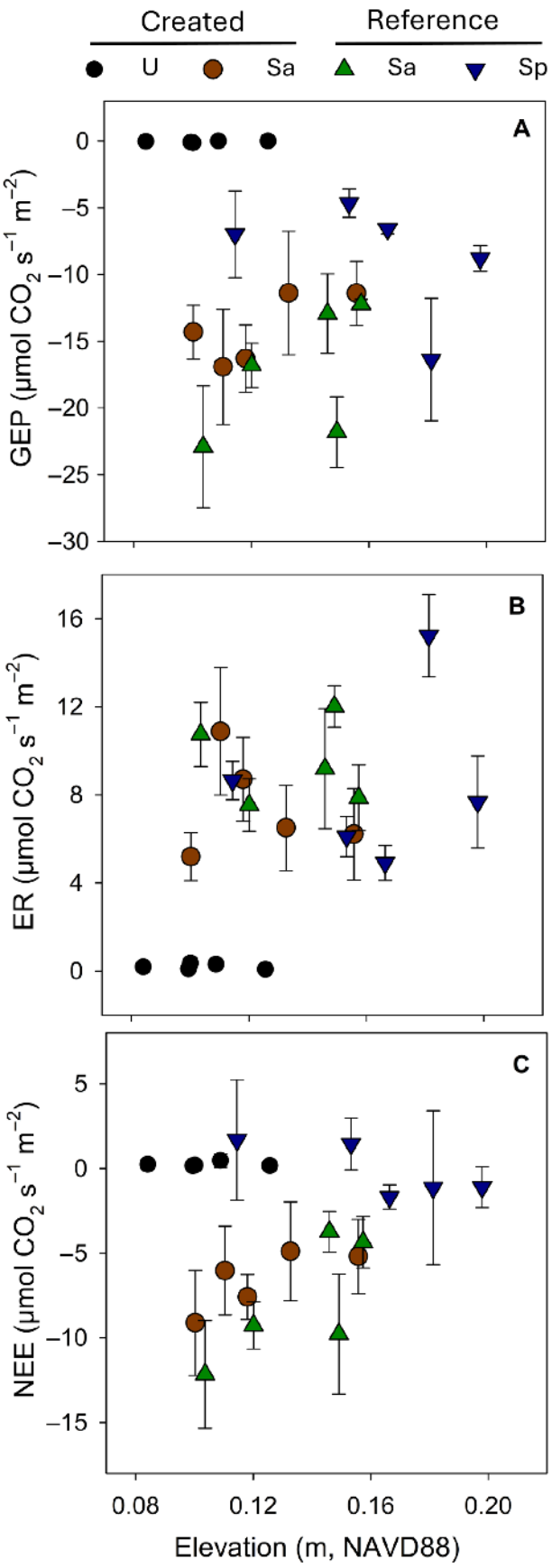


FIGURE 5 Gross ecosystem production (GEP), ecosystem respiration (ER), and net ecosystem exchange (NEE) of CO_2 in (A) May, (B) July, (C) September, and (D) the average across sampling dates (mean ± SE) in four habitat types: Unvegetated (U) and *Spartina alterniflora* (Sa) areas in a created marsh, and *S. alterniflora* (Sa) and *Spartina patens* (Sp) areas in a natural reference marsh in Sabine National Wildlife Refuge, Calcasieu, Louisiana. Different letters indicate significant differences within C flux and season based on post hoc Tukey HSD test.

increased. This suggests that, once vegetated, increasing plant biomass may not increase marsh function as a C sink due to concomitant increases in both productivity and respiration.

Within the reference marsh *S. alterniflora* habitat, GEP was greater as soil bulk density increased across seasons (Figure 8). For example, areas with a bulk density of ~0.19 g cm^{-3} had almost two times lower gross uptake of



CO_2 than sites with a bulk density of approximately 0.29 g cm^{-3} (Figure 8).

DISCUSSION

Wetland loss due to human impacts, storms, and relative sea level rise may be able to be mitigated by marsh restoration though how well restoration sites replicate important functions of much older natural marshes is still not well established. Marsh creation using dredged sediments is a common and widespread method of restoration along the Gulf coast of Louisiana where land loss is rapid and extensive (Bourne, 2000; Couvillion et al., 2017; Edwards & Proffitt, 2003; Walker et al., 1987). This strategy for replacing marsh habitat may be increasingly employed in other coastal areas where wetlands are being lost from human impacts and sea level rise. Focusing on C fluxes, this study illustrates the important role of marsh vegetation and environmental conditions such as marsh elevation that promote C uptake in both created and natural marshes. This study shows that while very different soil characteristics have the potential to affect C fluxes between created and reference marshes, C fluxes are instead dominated by vegetation and that when the same species is present, created marshes can function as an equivalent C sink. C fluxes did differ between *S. alterniflora* and *S. patens* in the natural reference marsh due primarily to lower early season GEP in *S. patens* areas.

Influence of plants on CO_2 fluxes in a created marsh

The presence of vegetation (i.e., *S. alterniflora*) increased C fluxes in the created marsh as compared to unvegetated sediments, converting the marsh areas from net C neutral to a net C sink, equivalent to that of *S. alterniflora*-dominated areas and exceeding that of *S. patens* areas in the natural reference marsh. The presence of *S. alterniflora* in the created marsh also seemed to facilitate algal colonization as chl *a* concentrations were three times greater within stands of *S. alterniflora* than in unvegetated areas. The contribution

FIGURE 6 Relationships between marsh elevation and (A) gross ecosystem production (GEP), (B) ecosystem respiration (ER), and (C) net ecosystem exchange (NEE) (mean ± SE) averaged across sampling dates in four habitat types: Unvegetated (U) and *Spartina alterniflora* (Sa) areas in a created marsh, and *Spartina alterniflora* (Sa) and *Spartina patens* (Sp) areas in a natural reference marsh in Sabine National Wildlife Refuge, Calcasieu, Louisiana.

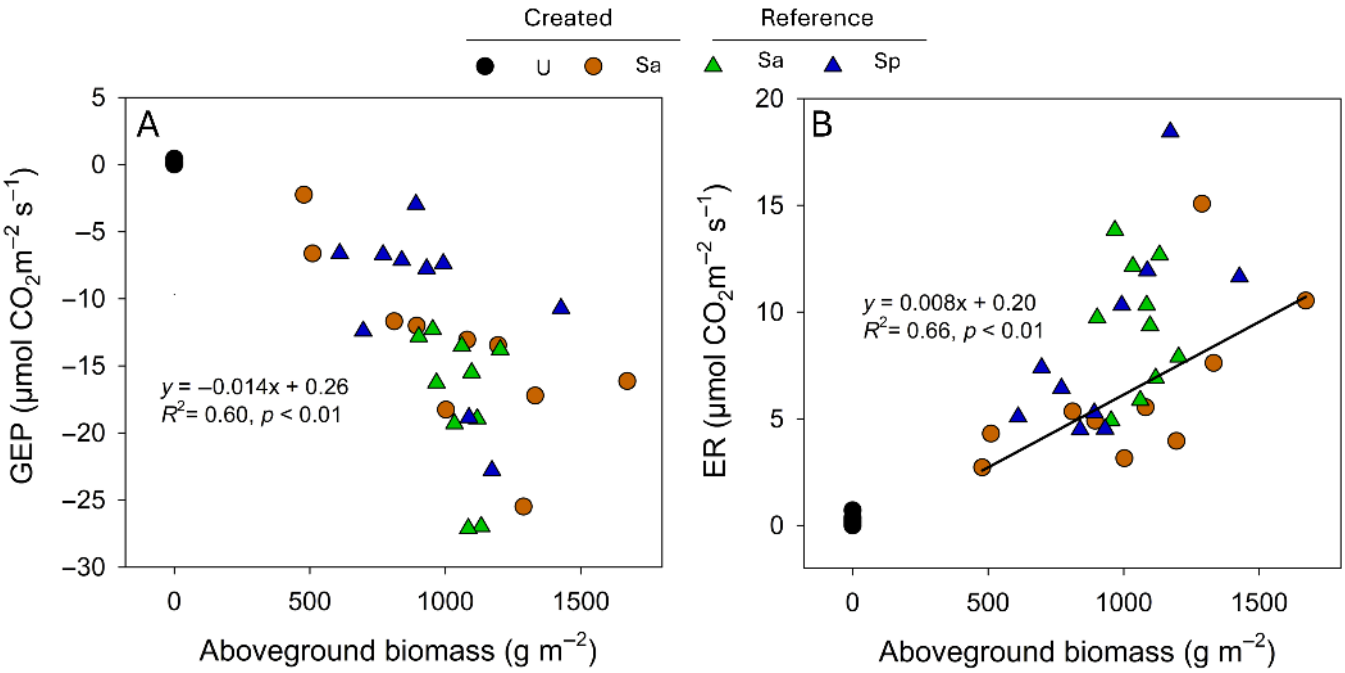


FIGURE 7 Relationships between estimated plant biomass and (A) gross ecosystem production (GEP) and (B) ecosystem respiration (ER) (means) across created and reference marsh habitats (U, unvegetated; Sa, *Spartina alterniflora*; and Sp, *Spartina patens*) in Sabine National Wildlife Refuge, Calcasieu, Louisiana.

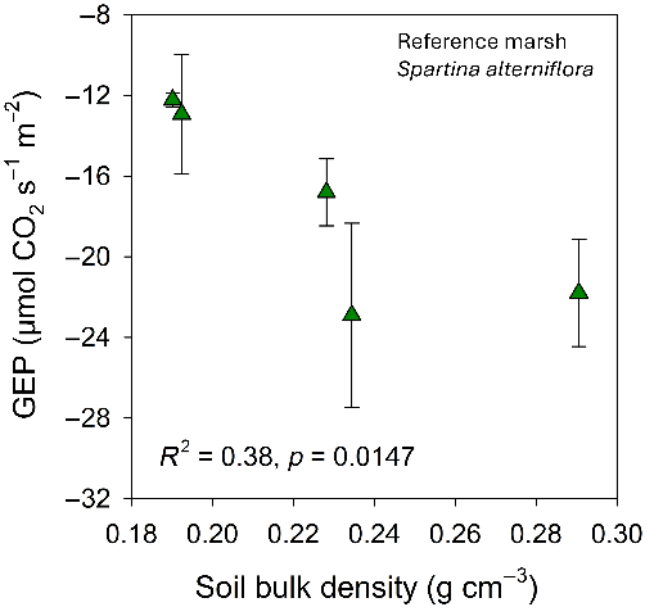


FIGURE 8 Relationship between soil bulk density and rate of gross ecosystem production (GEP) across the *Spartina alterniflora* habitat in the reference marsh in Sabine National Wildlife Refuge, Calcasieu, Louisiana. The regression included all data while the figure shows mean ± SE representing seasonal variability.

of edaphic algae to C fluxes was extremely low in unvegetated sediments but was likely greater in vegetated areas where they were more abundant (e.g., Gallagher & Daiber, 1974; Neubauer et al., 2000; Zedler, 1980). Chl *a* concentrations were greatest in the reference marsh *S. alterniflora* areas potentially owing to a more conducive sediment texture. The dredged material used to create these marshes have a relatively high clay content (45%–60%) that is prone to cracking upon desiccation as compared to natural marshes (29% clay; Abbott et al., 2019). Lower chl *a* concentration in the *S. patens* areas of the reference marsh is likely due to the dense canopy of thatch-limiting light availability as compared to less dense *S. alterniflora* stands (Hopkinson et al., 1980; Zedler, 1980).

The large difference in C fluxes between unvegetated and vegetated areas of the created marsh was almost entirely attributable to the high productivity of *S. alterniflora* that was large enough to offset ER, which was also greater than in the unvegetated habitat during most sampling periods. Microbial biomass in newly created marshes in this system was over four times lower than in natural reference marshes (Abbott et al., 2022) suggesting that soil efflux in the created marsh may be constrained by a low abundance of microbes. However, similar rates of respiration between vegetated areas of the created and natural marshes indicate that much of the respiratory CO_2 efflux can be attributed to root respiration. Root respiration in *S. alterniflora* has been shown to account for a greater percentage of soil respiration than microbial activity (Magenheimer et al., 1996) and *S. alterniflora* typically respires 30%–55% of the C fixed back to the atmosphere

diurnally (Spivak & Reeve, 2015). Others have also shown that non-vegetated marsh sediments have relatively low CO_2 fluxes compared with vegetated areas (Emery & Fulweiler, 2017; Sheng et al., 2015). In a salt marsh in Cape Cod, Massachusetts, unvegetated ponds were a small net source of CO_2 while low marsh *S. alterniflora*-dominated areas were a much larger net C sink (Moseman-Valtierra et al., 2016). This illustrates that disturbances that reduce marsh vegetation coverage reduces and potentially reverses the C sink function (Powell et al., 2020) and the importance of rapid vegetation establishment in restoration sites.

Rates of GEP and ER increased with plant biomass across vegetated habitats. Similarly, a positive relationship between aboveground biomass and NEE was found for a natural New England salt marsh (Emery & Fulweiler, 2017) and in a salt marsh in Connecticut (Barry et al., 2023). Greater aboveground biomass creates a larger photosynthetic area and thus gross capacity for CO_2 uptake. Aboveground biomass of *S. alterniflora* in the created marsh in this study ranged from ~500 to over 1500 g m^{-2}, with approximately 10 times greater CO_2 uptake in areas of higher biomass. ER also increased with aboveground biomass in the created marsh. However, in planted created marshes in North Carolina, biomass was unrelated to CO_2 fluxes because young marshes had a higher rate of CO_2 flux per unit biomass due to higher N availability and a greater photosynthetic rate (Cornell et al., 2007). In the present study, there were no significant differences in *S. alterniflora* biomass or CO_2 fluxes per gram of biomass between the created and reference marsh. PMN was generally lower in the created marsh than in the reference marsh, indicating greater availability of N with the higher SOM source in the reference marsh. Though not measured in this study, others have found a positive but nonlinear relationship between CO_2 fluxes and belowground biomass indicating a substantial influence of root respiration and/or root-associated microbial respiration on net CO_2 uptake (Moseman-Valtierra et al., 2016).

A notable difference between the unvegetated areas and the *S. alterniflora* clones was a large pool of available nitrogen (extractable NH_4^+-N) below 10 cm depth in the unvegetated areas, which was absent in the *S. alterniflora* patches. Nitrogen uptake by *S. alterniflora* clones in these created marshes enhances productivity, conferring a competitive advantage over *S. patens* at early successional stages (Muench & Elsey-Quirk, 2019). However, despite the potential higher nutrient availability and productivity of *S. alterniflora* in the created marsh, CO_2 fluxes were similar to those observed in the *S. alterniflora* habitat in the reference marsh.

Difference between reference and created *S. alterniflora* habitats

We hypothesized that *S. alterniflora* in created marshes would be more productive than populations growing in reference marshes associated with less competition (intra- and interspecific) and therefore a greater available nutrient pool in created marshes. However, we found that marsh type (created vs. reference) had little influence on CO_2 fluxes when the plant community remained constant (i.e., *S. alterniflora*) indicating that plant species effect on C fluxes dominated over the effects of differences in soil characteristics. SOM was low and nitrogen availability was high in the created marsh in comparison with the reference marsh. Together, this suggests that once created marshes are vegetated with the same species, there is the potential for C flux dynamics to reflect those of a natural marsh. However, aboveground biomass played an important role in rates of GEP and ER across marshes indicating that abiotic conditions that affect plant productivity will also influence C dynamics. For example, sandy, nutrient-poor conditions in marsh restoration sites in southern California resulted in lower stature plants (Zedler, 1993), which would likely lower the C sink capacity.

Do species matter?

Several studies have found differences in C fluxes among vegetation communities and zones in coastal marshes (Artigas et al., 2015; Barry et al., 2022; Moseman-Valtierra et al., 2016). However, because vegetation zones often differ in elevation and therefore, flooding frequency, and associated soil chemistry, the species effect is difficult to isolate. Nonetheless, in a natural salt marsh in Waquot Bay, Massachusetts, NEE was much lower in a *Juncus gerardi* and *D. spicata* high marsh zone than in low marsh *S. alterniflora* zone or a high marsh *P. australis* zone (Moseman-Valtierra et al., 2016). In contrast, eddy flux-based measures of CO_2 indicated that high marsh areas dominated by *S. patens* had greater NEE (16.8 mol CO_2 m^{-2} $year^{-1}$) than low marsh dominated by *S. alterniflora* in a natural marsh in New York (Artigas et al., 2015). In the present study, species occupied overlapping elevations allowing us to isolate the effect of species. Here, we found that at similar elevations, *S. alterniflora* in both the reference and created marshes is a greater C sink than *S. patens* in the reference marsh due to higher rates of GEP. *S. patens* was a source for CO_2 in May and had relatively low rates of GEP during all sampling events indicating low productivity overall. Elevation was a key driver of *S. patens* GEP in May with

higher rates at higher elevations suggesting that early season productivity of *S. patens* is affected by flooding. In a more temperate salt marsh in New Jersey, USA, *S. patens* was a greater C sink than *S. alterniflora* associated with maintenance of green stems for longer periods over the year (Artigas et al., 2015). Here, we found no seasonal effect on GEP or NEE of *S. alterniflora* and a low GEP of *S. patens* in the spring.

In contrast to the C flux dynamics found here, longer term soil C accumulation rates in these created marshes tended to be greater in areas dominated by high-density species such as *S. patens*, than in low-elevation *S. alterniflora* areas (Abbott et al., 2019). For *S. patens*, a greater aboveground accumulation of dead stem and leaf material that can be incorporated into the soil may contribute to high C accumulation and more efficient in trapping sediment (Fagherazzi et al., 2012) in this system. For *S. alterniflora*, much of the aboveground biomass is removed or decomposed over winter. Our study, however, did not include C flux measurements of *S. patens* in created marshes, which may differ from that in natural marshes. Nonetheless, together, these studies illustrate a high C sink capacity due to high GEP with initial colonization of *S. alterniflora* (present study) and high soil C accumulation rates over time in mid-marsh elevations with high-density species such as *S. patens* and *D. spicata* (Abbott et al., 2019). Longer-term soil C accumulation results from a combination of net C gas uptake, litter and belowground biomass accumulation, and sediment deposition, which influences the rate of burial (Czapla et al., 2020). Other studies have shown that allochthonous inputs of C and sediment allow soil C accumulation even when net CO_2 fluxes through plants and algae are negligible (Drexler et al., 2020).

Role of environmental factors

Marsh elevation had a significant influence on the productivity of *S. alterniflora* in both the created and reference marshes. and *S. patens* (in May). GEP in *S. alterniflora* habitats was more sensitive to elevation than *S. patens*-dominated areas and GEP was more sensitive to elevation than ER. Seasonal differences in marsh flooding also likely influenced C flux-elevation relationships. When the marsh was not flooded above the surface (May and July), the areas of highest C sinks in the *S. alterniflora* habitat occurred at lower elevations due to greater GEP. *S. alterniflora* occurred at elevations that ranged 6 cm. ER was variable across this elevation gradient, but GEP was maximized at low elevations when the marsh was not flooded above the surface. In September, when the marshes were flooded, NEE was similar across elevations in the *S. alterniflora* reference marsh community.

GEP of *S. patens* in May increased with increasing elevation resulting in *S. patens* acting less of CO_2 source at higher elevations. *S. patens* typically has greater above- and belowground biomass at higher elevations (Konisky & Burdirk, 2004; Snedden et al., 2015) and thus had a positive productivity response to less flooding. However, GEP in *S. patens* was not related to elevation in July and September when the community was a CO_2 sink and NEE neutral, respectively.

In general, flooding can reduce NEE in salt marshes by decreasing plant and soil CO_2 fluxes (Kathilankal et al., 2008; Moffett et al., 2010). Exposed to a higher tidal range than in the present study, photosynthesis of *S. alterniflora* can decline 66% under flooded conditions, causing a 46% reduction in NEE (Kathilankal et al., 2008). Though we found no influence of elevation on ER, soil CO_2 flux can be depressed under flooding as anaerobic conditions become more prominent reducing microbial activity (Magenheimer et al., 1996; Nyman & Delaune, 1991). Flooding can reduce ER and indirectly influence CO_2 uptake through changes in temperature and vapor pressure deficit (Knox et al., 2018).

We found no influence of soil nitrogen availability on C fluxes, but *S. alterniflora* in the reference marsh was more productive in areas of higher soil bulk density suggesting that increasing mineral sediment in natural marshes will increase productivity and C sink capacity. As compared to *S. alterniflora* marshes in Barataria Bay, soil bulk densities in the reference marsh in this system were relatively low (DeLaune et al., 1979). In Barataria Bay, aboveground biomass increased linearly with an increase in soil bulk density from 0.19 to 0.37 g cm^{-3} (DeLaune et al., 1979), while the highest bulk density in the present study was 0.29 g cm^{-3}. Many natural marshes in Louisiana are struggling to keep pace with rising sea levels, particularly in the Chenier Plain region (Jankowski et al., 2017). Highly organic marshes that are subject to high rates of relative sea level rise, tend to increase productivity with an increased input of mineral sediment conveying a higher soil bulk density (DeLaune et al., 1979).

Conclusion

Vegetation was the main determinant of marsh CO_2 fluxes, while differences in sediment characteristics between created and natural marshes seemed to have relatively limited effects on CO_2 fluxes. Vegetation can rapidly colonize created marshes with plant biomass quickly reaching that of natural marshes, but sediment characteristics generally take much longer to develop

(Craft et al., 2003; Edwards & Proffitt, 2003). In the natural reference marsh, C sink capacity of *S. alterniflora* was enhanced by lower elevations and higher soil bulk density indicating that flooding and greater mineral sediment can enhance productivity and C assimilation in natural marshes. We also found species differences in C fluxes in the reference marsh with a low early spring GEP in *S. patens* that is enhanced at higher elevations. Overall, our study illustrates that CO_2 fluxes in created coastal marshes depend on vegetation establishment and productivity and have the potential to reach reference levels in a relatively short amount of time, allowing created marshes to sequester CO_2 at similar rates to natural marshes.

AUTHOR CONTRIBUTIONS

A. Muench and T. Elsey-Quirk conceived the ideas and designed the methodology. A. Muench collected the data. A. Muench and T. Elsey-Quirk analyzed the data. A. Muench and T. Elsey-Quirk led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Quirk et al., 2024) are available from Dryad: https://doi.org/10.5061/dryad.xsj3tx9qt.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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