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Buried hurricane legacies: increased nutrient limitation and decreased root biomass in coastal wetlands

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Abstract. Plant identity and cover in coastal wetlands is changing in worldwide, and many subtropical salt marshes dominated by low-stature herbaceous species are becoming woody mangroves. Yet, how changes affect coastal soil biogeochemical processes and belowground biomass before and after storms is uncertain. We experimentally manipulated the percent mangrove cover (*Avicennia germinans*) in 3 × 3 m cells embedded in 10 plots (24 × 42 m) comprising a gradient of marsh (e.g., *Spartina alterniflora*, *Batis maritima*) and mangrove cover in Texas, USA. Hurricane Harvey made direct landfall over our site on 25 August 2017, providing a unique opportunity to test how plant composition mitigates hurricane effects on surface sediment accretion, soil chemistry (carbon, C; nitrogen, N; phosphorus, P; and sulfur, S), and root biomass. Data were collected before (2013 and 2016), one-month after (2017), and one-year after (2018) Hurricane Harvey crossed the area, allowing us to measure stocks before and after the hurricane. The accretion depth was higher in fringe compared with interior cells of plots, more variable in cells dominated by marsh than mangrove, and declined with increasing plot-scale mangrove cover. The concentrations of P and $\delta^{34}S$ in storm-driven accreted surface sediments, and the concentrations of N, P, S, and $\delta^{34}S$ in underlying soils (0–30 cm), decreased post-hurricane, whereas the C concentrations in both compartments were unchanged. Root biomass in both marsh and mangrove cells was reduced by 80% in 2017 compared with previous dates and remained reduced in 2018. Post-hurricane loss of root biomass in plots correlated with enhanced nutrient limitation. Total sulfide accumulation as indicated by $\delta^{34}S$, increased nutrient limitation, and decreased root biomass of both marshes and mangroves after hurricanes may affect ecosystem function and increase vulnerability in coastal wetlands to subsequent disturbances. Understanding how changes in plant composition in coastal ecosystems affects responses to hurricane disturbances is needed to assess coastal vulnerability.

Key words: disturbance; Hurricane Harvey; marsh–mangrove ecotone; nutrient biogeochemistry; pulse dynamics; sediment deposition.

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Introduction

A fundamental challenge in ecology is to understand how disturbance pulses (Junk et al. 1989, Odum et al. 1995, Polis et al. 1997, Yang et al. 2008, 2010) and subsidy-stress gradients drive ecosystem structure and function (Odum et al. 1979, Wilson et al. 2019). At the same time, climate change is driving global redistribution of species and altering emergent properties of ecosystem structure and function (Walther et al. 2002, Chen et al. 2011, Lenoir and Svenning 2014). In coastal landscapes, climate and land-use changes are transforming species composition in coastal landscapes (Day et al. 2008, Coverdale et al. 2013), as many species are expanding their ranges poleward, creating novel ecotones of communities in transition (Chen et al. 2011, Alexander et al. 2015). Mangroves, for example, are encroaching into marshes through range expansion along the temperate–tropical ecotone (Cavanaugh et al. 2014, Yando et al. 2016, Kelleway et al. 2017). In some regions, mangrove latitudinal expansion and contraction is strongly influenced by the frequency and intensity of extreme cold events (Osland et al. 2013, Saintilan et al. 2014, Coldren et al. 2019). In these transitional regions, small temperature changes can spur nonlinear expansion or contraction of mangrove forest area (Osland et al. 2017, Saintilan et al. 2018). Increased minimum temperature drives mangrove expansion, whereas freeze events cause a dieback and reduction in mangrove cover (Perry and Mendelssohn 2009, Ross et al. 2009, Cavanaugh et al. 2014).

Mangrove expansion into herbaceous marshes can alter above- and belowground soil organic and inorganic matter concentrations. Mangroves increase sediment retention and accretion, reduce erosion, attenuate waves, and increase carbon and nutrient storage (Friess et al. 2011, Comeaux et al. 2012, Kelleway et al. 2017, Chen et al. 2018, Charles et al. 2020, Pennings et al. 2021). Mangrove roots stabilize the soil substrate and increase elevation, and the prevention of vertical erosion and accumulation of slower-decaying organic matter increase soil carbon content in mangroves (Gedan et al. 2011, Charles et al. 2020). At the landscape level, increases in mangrove cover and stand height can both attenuate and increase retention of allochthonous subsidies (Doughty et al. 2017, Charles et al. 2020). Increased mangrove cover enhances wetland carbon storage through higher above- and belowground biomass, accumulation of more recalcitrant organic matter, and reduced surface organic matter breakdown compared with marshes (Charles et al. 2020).

Although coastal wetlands attenuate wind and wave energy associated with storms (Danielsen et al. 2005, Gedan et al. 2011, Zhang et al. 2012), it is unclear how high-energy storms impact soil processes in wetlands of varying marsh and mangrove cover (Alongi 2008, Doughty et al. 2017). Hurricanes are large-scale pulsing events driving structural and functional changes in coastal ecosystems (Michener et al. 1997, Lugo 2008). In the marsh–mangrove ecotone, mangroves generally prevent more soil erosion and are prone to more physical damage from hurricanes than marsh vegetation, which may limit longer-term shoreline erosion protection (Armitage et al. 2020). Black mangrove aboveground regrowth can occur immediately following a hurricane (Armitage et al. 2020), but the impacts of hurricane-related stress on soil chemical concentrations and belowground processes are uncertain. In particular, delayed mortality has been observed in mangroves following hurricanes (Radabaugh et al. 2020), suggesting that hurricanes create long-lasting legacies in soils or plant physiology.

Here, we tested how plant species identity and cover in coastal wetlands at the marsh–mangrove ecotone affected surface sediment accretion and chemistry, soil chemistry, and root biomass before (Charles et al. 2020) and after Hurricane Harvey crossed directly over the marsh. We expected a high-magnitude hurricane such as Hurricane Harvey to transport large sediment loads into coastal wetlands (Tweel and Turner 2012). Our analyses were guided by the following predictions: (1) The quantity of storm sediment deposited during the hurricane would decrease along a gradient of mangrove cover because mangroves can attenuate allochthonous matter during events (Charles et al. 2020); (2) sediments transported by the storm would have higher carbon and nutrient (nitrogen [N], phosphorus [P], and sulfur [S]) concentrations than pre-storm accreted sediments, as has been observed with marine wrack deposition and other storms in the Gulf of Mexico (Castañeda-Moya et al. 2010, Castañeda-Moya et al. 2020, Charles et al. 2020); (3) marshes would have greater chemical changes to soils than mangroves; and (4) higher total sulfide accumulation in soils as indicated by $\delta^{34}S$ would occur where plant stress and sedimentation were highest, reflecting reduced soil conditions (Holmer and Hasler-Sheetal 2014). We also anticipated (5) lower root biomass where storm-driven soil nutrients increased (i.e., fringe > interior) because allochthonous subsidies may enhance aboveground and reduce belowground growth (Poorter and Nagel 2000, Deegan et al. 2012). One year following the hurricane, we predicted that (6) the lowest root biomass in plots would be where there was the greatest vegetation cover damage (Armitage et al. 2020), because plant energy would be allocated to recovery aboveground.

Methods

Study site and experimental plots

This research was conducted in the microtidal saline wetlands of Harbor Island, Port Aransas, Texas, USA (27.86° N, 97.06° W). Mangroves have been there since at least the 1930s (Montagna et al. 2011). Mangrove expansion and contraction since the mid-1900s resulted in reversals in dominance at the marsh–mangrove ecotone (Comeaux et al. 2012, Osland et al. 2017). The most recent mangrove expansion followed freeze events from 1980 to 1989 that caused widespread mangrove contraction (Armitage et al. 2015). In 2012, the wetlands were predominately occupied by black mangroves (*Avicennia germinans*); approximately 10% of total plant cover then was marsh species (mostly *Spartina alterniflora*, *Batis maritima*, *Salicornia*, and *Sarcocornia* spp.; Guo et al 2017).

We assessed the outcome from different scenarios of mangrove expansion and contraction by removing mangroves to create a gradient of marsh and mangrove cover (Fig. 1). We established 10 large coastal plots in 2012 (24 m parallel to the coastline and extending 42 m inland) in wetlands of similar geomorphology located along the Lydia Ann Shipping Channel (Guo et al. 2017). We created 112 cells that were 3×3 m within each of the 10 plots. We then removed enough of the aboveground biomass in randomly selected cells within the 10 plots to create 10 different amounts of plant cover for the whole plot: 0%, 11%, 22%, 33%, 44%, 55%, 66%, 77%, 88%, and 100%. Marsh vegetation naturally recolonized in cells where mangroves had been removed (Guo et al. 2017, Charles et al. 2020). Some interior marsh ($n = 8$) and fringe mangrove cells ($n = 3$) did not revegetate or apparently eroded after the hurricane. We refer to all cells where mangroves were removed as marsh cells and all cells where mangroves were left intact as mangrove cells hereafter. In each plot, we randomly sampled from four 3×3 m cells along the coastal fringe (cells in the front third of each plot, 3–9 m from the channel) and from four 3×3 m cells within the plot interior (cells in the remaining two thirds of each plot). Replicate cells were all marsh (in the 0% mangrove plot), all mangrove (in the 100% mangrove plot), or half marsh and half mangrove (in mixed plots), that is, two marsh and two mangrove cells in both fringe and interior zones. We sampled a total of $n = 80$ cells.

Hurricane Harvey: hydrology and storm surge

Hurricane Harvey made landfall on 25 August 2017 directly on our site as a Category 4 hurricane (Fig. 1) with sustained hurricane-force wind speeds exceeding 119 kph (gusts up to 225 kph) for approximately 6 h (Blake and Zelinsky 2018). A tide gauge at Port Aransas, ~3.5 km from the experimental plots, recorded a storm surge of 1.6 m above MLLW (NOAA 2019), and estimates of storm surge based on debris deposition and other flood evidence indicated a storm surge of up to 2.4 m (USGS 2019). Major flooding (0.8 m above MLLW) persisted for approximately 6 h. All methods and analyses in this study refer to three sampling periods: pre-hurricane (2013–2016; Charles et al. 2020), immediately post-hurricane (October 2017), and after one year of recovery post-hurricane (November 2018).

Surface sediment accretion

In 2013, four years before Hurricane Harvey, we randomly installed feldspar marker horizons (0.5 m^2; Cahoon and Turner 1989) in each plot ($n = 4$ marsh cells and $n = 4$ mangrove cells per plot, $n = 80$ in total). We measured accretion depth (cm) onto feldspar marker horizons following Cahoon and Turner (1989) in 2015 (pre-hurricane,

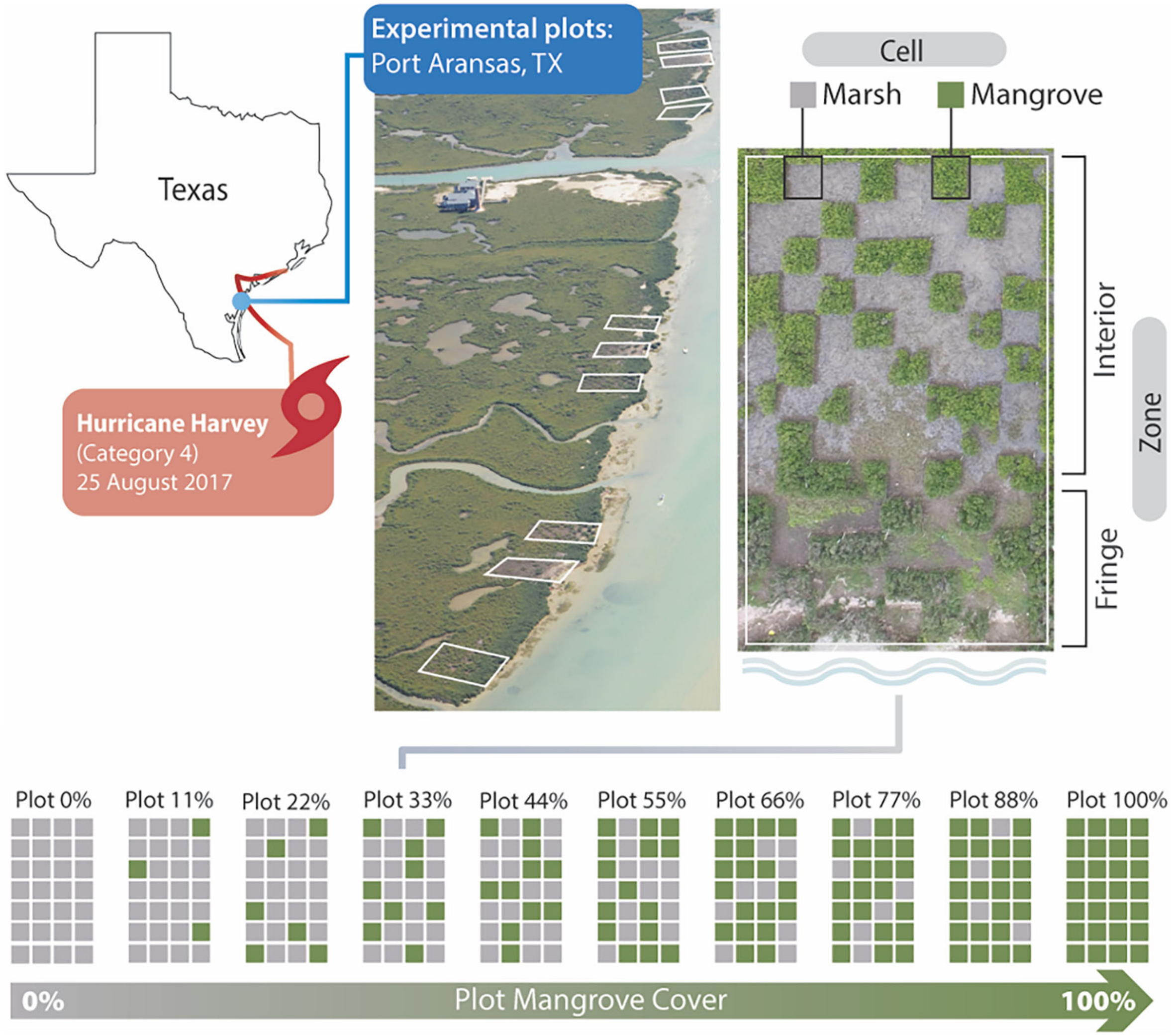

Fig. 1. Aerial imagery of coastal experimental plots (indicated by white outlines) on Harbor Island, Port Aransas, Texas, USA. The percent values indicate the maintained mangrove cover of each 24 × 42 m plot (n = 10) comprised of 3 × 3 m^2 monospecific marsh or mangrove cells (n = 112 cells/plot). The red line on the map of Texas denotes the relative path of Hurricane Harvey, which made direct landfall on our sites on 25 August 2017 as a Category 4 hurricane. Due to space limitations, graphic image of cells in each plot in the bottom panels of the figure represents half of the actual 3 × 3 m^2 cells in plots.

22 months post-installation, n = 47) and 2017 (immediately post-hurricane, 52-months post-installation, n = 19). Feldspar marker horizons could no longer be identified in 2018.

Accreted surface sediment and soil chemistry

In 2015, 2017, and 2018, we collected soil cores (5 cm diameter × 30 cm depth) in each of the same randomized cells where feldspar marker horizons were established (n = 8 per plot) to measure chemistry in the accreted surface sediments and soils. We separated the accreted surface sediments from lower soil layers if feldspar marker horizons were present. If not present, then the entire core was treated as a soil sample (assuming no accreted surface sediments). We removed roots from the accreted surface sediments and soils, and cores were homogenized and subsampled for chemical analyses. Subsamples were dried at 60°C to a constant dry mass. We ground and homogenized portions with an 8000-D ball mill (Spex SamplePrep, Metuchen, New Jersey, USA). We measured the percentage of carbon (C) and percentage of nitrogen (N) using a CHN Analyzer (PerkinElmer 2400, Waltham, Massachusetts, USA). We determined the percentage of phosphorus (P) using acid hydrolysis followed by spectrophotometric analysis to estimate phosphate concentration of the extract (Fourqurean et al. 1992). A Thermo-Electron Delta V Mass Spectrometer via ConFlo III Interface (Thermo Fisher Scientific, Waltham, Massachusetts, USA) was used to measure the %S and stable isotopes. The ratios of heavy to light stable isotopes are expressed as δ to indicate relative depletion (−) or the enrichment (+) of the heavy isotope compared with the lighter isotope relative to a standard, according to the formula: δX (‰) = $([R_{\text{sample}}/R_{\text{standard}}] - 1) \times 10^3$, where X is ^{34}S and R is $^{34}\text{S}{:}^{32}\text{S}$. Results are presented as deviations from a standard (Canyon Diablo troilites for S). Repeatability was $\delta^{34}\text{S} \pm 0.3$‰.

Marsh and mangrove root biomass

We collected a second set of soil cores (5 cm diameter × 30 cm depth) to measure root biomass. Pre-hurricane (2013), we measured root biomass in four fringe and four interior cells of each of six of the ten plots (0%, 22%, 33%, 55%, 66%, and 100% mangrove; $n = 48$ cells; Charles et al. 2020). Post-hurricane (2017 and 2018), we quantified marsh and mangrove root biomass in four fringe and four interior cells in all 10 plots ($n = 80$ cells). We separated live roots (1–20 mm diameter) using a 1-mm mesh sieve, identified them as living or dead based on color, turgidity, and buoyancy, and collected them for root biomass measurements. We sorted live roots into two size classes: fine (1–6 mm diameter) and coarse roots (>6 mm diameter). Living roots have been empirically identified using these physical attributes in both marsh (Connor and Chmura 2000) and mangrove (Komiyama et al. 1987) vegetation. We determined the organic content of live roots by calculating ash-free dry mass (loss on ignition in a muffle furnace at 500°C for 5 h). We calculated belowground biomass using the equation from Karam (1993):

$$\text{root biomass}\ (\text{g C/m}^2) = \frac{\text{root dry mass (g)} \times \text{C content (\%)}}{\text{core area (m}^2)} \quad (1)$$

Data analyses

Although a lack of spatial replication of our plot-scale mangrove cover treatments violates assumptions of inferential statistics (Hurlbert 1984), the multiple treatment cells and plots of our experiment and inclusion of measurements from pre- and post-hurricane years were necessary to capture integrated ecosystem-scale responses to vegetation type and cover, and hurricane impacts.

To test whether hurricane storm effects on accreted sediments varied along a gradient of mangrove cover in marsh and mangrove cells (predictions 1, 2), we fit linear models of accretion depth and chemistry collected from feldspar marker horizons to cell-scale vegetation type (marsh, mangrove) nested within continuous effects of plot-scale mangrove cover (0–100%) pre- and post-hurricane. We used adjusted R^2 to assess goodness of fit of linear models. Variance in post-hurricane accretion depth in marsh and mangrove cells was compared using Welch's two-sample t test.

To test hurricane storm effects on the chemistry of soils (predictions 3, 4) and root biomass (predictions 5, 6) along a gradient of mangrove cover in marsh and mangrove cells, we built hierarchical linear mixed-effects (LME) models using the lme4 package in R (Bates et al. 2015). Specifically, we assessed nested factors (cell-scale vegetation type [marsh, mangrove] and cell location within plot [fringe, interior], and continuous effects of plot-scale mangrove cover [0–100%]), categorical effects of hurricane (pre, post), and random effects of year. Mixed-effects models are appropriate statistical tools for analyzing data collected across multiple spatial and temporal scales (Zuur et al. 2009). We included fixed and random factors in models to allow us to assess independent variables and to account for hierarchical structure (spatial nestedness; Zuur et al. 2009). We used conditional R^2 to assess goodness of fit for mixed-effects models (includes variance of fixed effects and random effects; Nakagawa and Schielzeth 2013). Due to the large number of variance–covariance parameters in these complex mixed-effects models, there were some instances of singular fits for random but not fixed factors. Data files and model code are provided for further information (Data S1: Harvey RAPID Sediment Soils Roots).

All response variables were $\log_{10}$-transformed where necessary to reduce heteroskedasticity of variances, and all transformed data were standardized to *z*-scores to center the data and enhance interpretation among continuous predictors (Gelman and Hill 2006). All statistical analyses were performed using RStudio v.1.3.1093 (R Core Team 2020).

Results

Surface sediment accretion

The surface sediment accretion depth (cm) was highest after the hurricane compared with before the hurricane and was lower in mangrove cells (Table 1). Accretion depth was 2.3× greater in marsh cells than mangrove cells after the hurricane (Table 1, Fig. 2A). The accretion depth decreased in mangrove cells with plot-scale mangrove cover before and after the hurricane (Table 1, Fig. 2A). Post-hurricane cell-scale accretion depth was more variable in marsh (CV = 72%) than mangrove cells (CV = 17%; $t = 2.44$, df = 8.87, $P = 0.04$; Table 1, Fig. 2A).

Accreted surface sediment and soil chemistry

The concentrations of S (%) in the accreted surface sediments were similar in fringe and in interior marsh and mangrove cells of all plots before and after the hurricane (Table 1, Fig. 2B). The isotopic sulfur (δ^{34}S) (‰) values in accreted surface sediments were reduced in marsh and mangrove cells in all plots post-hurricane compared with before the hurricane (Table 1, Fig. 2C). The concentrations (%) of C and N in accreted surface sediments were greater in mangrove cells at higher plot-scale mangrove cover both pre- and post-hurricane (Table 1, Fig. 2D, E). Concentrations of P (%) in accreted surface sediments were reduced by nearly 50% post-hurricane (Table 1, Fig. 2F).

The chemical concentrations of soils (0–30 cm below the marker horizons) were variable relative to cell- and plot-scale vegetation composition and generally decreased post-hurricane. The soil %C was similar among interior and fringe marsh and mangrove cells in all plots pre- and post-hurricane (Table 2; Appendix S1: Fig. S1). The soil N (%) decreased slightly post-hurricane (Table 2, Fig. 3). The soil %P decreased dramatically post-hurricane in all plots, especially in fringe mangrove cells and interior marsh cells plots in plots with lower mangrove cover (Table 2, Fig. 4). The soil S (%) decreased post-hurricane and was highly variable among interior and fringe marsh and mangrove cells in all plots (Table 2; Appendix S1: Fig. S2).

Despite reduction in isotopic sulfur (δ^{34}S; ‰) concentrations in some soils post-hurricane, soil δ^{34}S remained oxidized in fringe and interior mangrove cells of plots (Table 2, Fig. 5B). More depleted δ^{34}S values were observed in coastal (fringe) marsh cells one month after the hurricane (2017), and by one year post-hurricane (2018), δ^{34}S values were further depleted in both marsh and mangrove fringe soils (Fig. 5A, B).

Marsh and mangrove root biomass

Pre-hurricane, total (coarse and fine) live root biomass (0–30 cm; g C/m^2) was higher in interior and fringe mangrove cells of plots than in fringe marsh cells, and increased with plot-scale mangrove cover (Fig. 6). Biomass was 1.9× higher in mangrove than in marsh cells and 3.7× higher in interior than in fringe cells (Fig. 6). Coarse and fine root biomass decreased post-hurricane in both marsh and mangrove cells and in fringe and interior cells of plots (Table 2, Fig. 6).

Discussion

Our results indicate that although plant composition influenced physical processes during the hurricane, the chemistry accreted sediments and soils in marshes and mangroves were largely reduced and homogenized by Hurricane Harvey. Storm surges often bring pulses of sediments that are attenuated and filtered by coastal wetlands. We expected that the storm surge from Hurricane Harvey transported large sediment loads into coastal wetlands as has been observed with other storms (Castañeda-Moya et al. 2010, Tweel and Turner 2012, Castañeda-Moya et al. 2020). We predicted that the aerial roots and branching stems of mangrove trees would promote more deposition than in marsh vegetation and that the quantity of storm sediment deposited during the

Table 1. Linear model results of cell-scale vegetation type (marsh, mangrove) nested within continuous effects of plot-scale mangrove cover (0–100%) from surface sediment accretion depth and accreted surface sediment chemistry responses to Hurricane Harvey.

						Model	
Variable	Factor	Estimate	SE	*t*	*P*	Adj. R^2	*P*
Accretion depth (cm)	Intercept	0.476	0.252	1.89	0.06	0.13	<0.01
	Hurricane	−0.303	0.132	−2.30	**0.03**		
	Cover:Mangrove	−0.009	0.004	−2.37	**0.02**		
	Cover:Marsh	−0.002	0.005	−0.38	0.71		
%C	Intercept	−0.279	0.249	−1.12	0.27	0.15	<0.01
	Hurricane	−0.134	0.130	−1.03	0.31		
	Cover:Mangrove	0.011	0.004	2.79	**0.01**		
	Cover:Marsh	−0.001	0.005	−0.28	0.78		
%N	Intercept	−0.355	0.259	−1.37	0.18	0.08	0.04
	Hurricane	0.038	0.136	0.28	0.78		
	Cover:Mangrove	0.001	0.004	2.42	**0.02**		
	Cover:Marsh	0.001	0.006	0.11	0.91		
%P	Intercept	−0.533	0.220	−2.43	**0.02**	0.34	<0.001
	Hurricane	0.666	0.115	5.79	**<0.001**		
	Cover:Mangrove	0.005	0.003	1.57	0.12		
	Cover:Marsh	0.004	0.005	0.84	0.41		
%S	Intercept	−0.105	0.260	−0.41	0.69	0.07	0.05
	Hurricane	−0.078	0.136	−0.57	0.57		
	Cover:Mangrove	0.006	0.004	1.65	0.11		
	Cover:Marsh	−0.005	0.006	−0.85	0.40		
δ^{34}S (‰)	Intercept	−0.386	0.194	−1.99	**0.05**	0.49	<0.001
	Hurricane	0.765	0.102	7.54	**<0.001**		
	Cover:Mangrove	0.002	0.003	0.77	0.45		
	Cover:Marsh	−0.001	0.004	−0.22	0.83		

Notes: Bolded values denote significance of $P < 0.05$ using $\alpha = 0.05$.

SE, standard error. Adjusted R^2 was used to assess goodness of fit for models for each parameter. Samples were collected from 0.5-m^2 feldspar marker horizons that were established in 2013 in marsh and mangrove cells in plots ($n = 10$) that span a gradient in percent mangrove cover (0%, 11%, 22%, 33%, 44%, 55%, 66%, 77%, 88%, and 100%). Data from pre-hurricane were collected in 2015 ($n = 47$ total; see Charles et al. 2020). Data from post-hurricane were collected in 2017 ($n = 19$). Feldspar markers could not be located in 2018.

hurricane would increase along a gradient of plot-scale mangrove cover. However, these predictions were not fully supported. Instead, storm surge sediment accretion was highest and most variable in marsh cells and decreased in mangrove cells with plot-scale mangrove cover (Table 1). Relative to the marsh cells, mangrove cells likely promoted autochthonous sediment retention and may have inhibited storm-driven sediment deposition and erosion (Armitage et al. 2020, Charles et al. 2020, Pennings et al. 2021). Our observations suggest that mangroves trap debris at the very front of plots and of mangrove cells and that this likely inhibited the transport of allochthonous sediments into and through areas with high mangrove cover (Guo et al. 2017). Our predictions that (1) storm-driven sediment accretion would have higher carbon and nutrient [nitrogen (N), phosphorus (P), and sulfur (S)] content than pre-storm accreted sediments (Castañeda-Moya et al. 2010) and (2) marshes would have greater chemical changes to accreted surface sediments and soils than mangroves were partially supported. We measured reduced nutrient, but not carbon concentrations, in accreted surface sediments and soils, and these persisted one year after the hurricane. We anticipated a high sulfide (δ^{34}S) accumulation, as indicated from depleted δ^{34}S content in accreted surface sediments and soils, where plant stress and sedimentation reduced soil conditions (Holmer and Hasler-Sheetal 2014), which we observed in marsh cells across plot-scale mangrove cover, especially in the eroded fringes of plots (Armitage et al. 2020, Pennings et al. 2021). We predicted lowest root biomass in treatments of

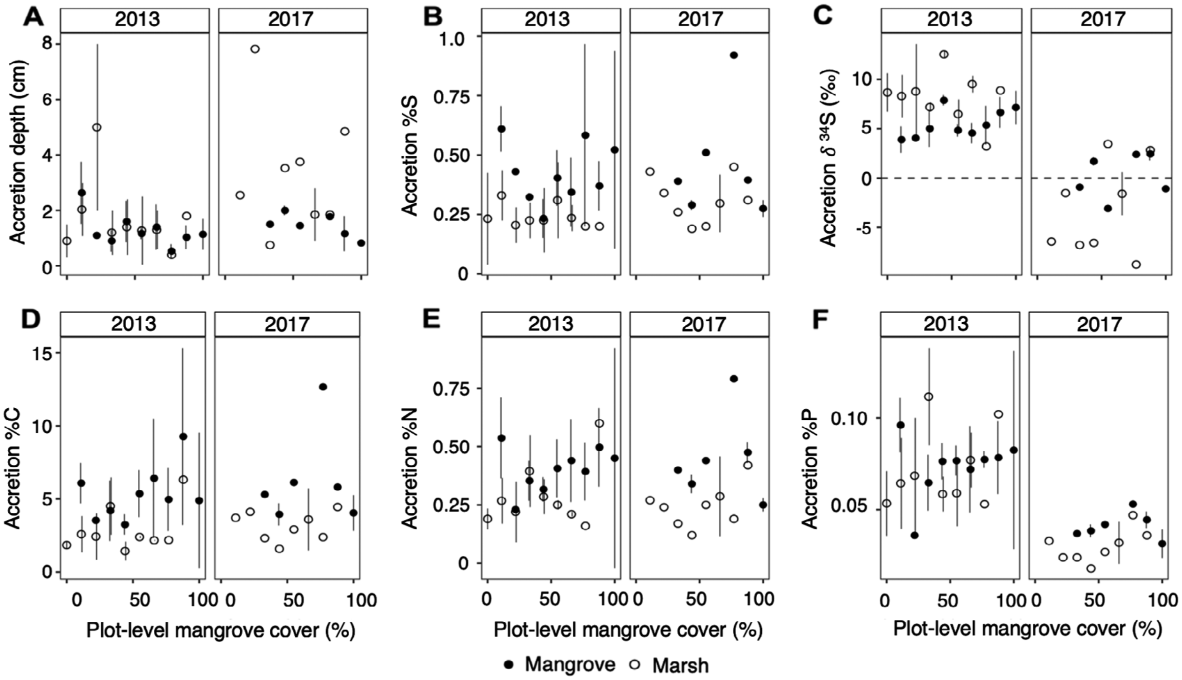

Fig. 2. Measured surface sediment accretion (cm; A) and its chemical concentrations (%S, B; δ^{34}S, ‰, C; %C, D; %N, E; and %P, F) from coastal wetland plots in Port Aransas, Texas, USA, from dates pre- (2013) and post-Hurricane Harvey (2017). Symbols correspond to wetland cells (3 × 3 m) of different vegetation types (marsh, open; mangrove, filled) along a gradient in plot-level percent mangrove cover.

greatest vegetation cover damage (Armitage et al. 2020), but there was a coincidental widespread depletion in δ^{34}S and lower root biomass across both marsh and mangrove cells in all plots.

Sediment deposition by hurricanes into coastal wetlands is well documented (Nyman et al. 1995, Cahoon et al. 1996) and may enhance surface elevation and carbon burial relative to eustatic sea level rise (McKee and Cherry 2009, Smoak et al. 2013, Baustian and Mendelssohn 2015). Sediment deposition may bury mangrove and marsh roots (Ellison 1999, Macreadie et al. 2013) depending on geomorphic setting, hurricane path, and type of sediment deposited (Smith et al. 2009). However, in our study, mangrove cells inhibited surface sediment accretion post-hurricane. Results from other studies in these same wetlands found that mangrove cover enhanced shoreline retention by reducing vertical and fringe erosion, which is likely attributed to greater soil strength in mangrove cells (Armitage et al. 2020, Pennings et al. 2021). Coastal vegetation species differentially modify soil strength through organic detritus input, and greater root biomass and organic content in these mangrove cells (Charles et al. 2020), and may lower soil bulk density and increase sediment stability (Feagin et al. 2009). Our research suggests that mangroves function as critical biophysical filters on multiple spatial scales despite storm-driven changes in sediment biogeochemistry, retaining accreted sediments along coastal fringe margins (Charles et al. 2020) and reducing sediment even at low plot-scale mangrove cover (Pennings et al. 2021). Increases in mangrove cover in coastal wetlands may therefore enhance physical shoreline retention and reduce storm sediment and wrack deposition (Armitage et al. 2020, Pennings et al. 2021).

Although mangroves provided shoreline protection through reduced erosion, hurricane storm surge increased nutrient limitation and stress in both marshes and mangroves. Soils in this region are primarily inorganic and sand-rich (7% C content) with higher organic content in mangrove

Table 2. Hierarchical linear fixed-effects model outputs comparing nested factors (cell-scale vegetation type [marsh, mangrove] and cell location within plot [fringe, interior], and continuous effects of plot-scale mangrove cover [0–100%]), categorical effects of hurricane (pre, post), and random effects of year from soil (0–30 cm) chemistry and total live root biomass responses to Hurricane Harvey.

Variable	Factor	Estimate	SE	df	t	P	Model conditional R^2
Soil %C	Intercept	−0.032	0.225	5.06	−0.14	0.89	0.12
	Hurricane	0.100	0.194	2.78	0.52	0.64	
	Cover:Fringe:Mangrove	0.004	0.003	182.97	1.32	0.19	
	Cover:Interior:Mangrove	0.003	0.003	182.92	0.99	0.32	
	Cover:Fringe:Marsh	−0.001	0.004	183.34	−0.32	0.75	
	Cover:Interior:Marsh	−0.003	0.004	182.87	−0.95	0.35	
Soil %N	Intercept	0.022	0.143	5.06	−0.14	0.89	0.13
	Hurricane	0.329	0.088	2.06	3.75	0.06	
	Cover:Fringe:Mangrove	0.003	0.003	182.70	1.24	0.22	
	Cover:Interior:Mangrove	0.001	0.003	182.40	0.42	0.68	
	Cover:Fringe:Marsh	−0.001	0.004	184.20	−0.22	0.83	
	Cover:Interior:Marsh	−0.004	0.004	182.20	−1.05	0.30	
Soil %P	Intercept	0.157	0.082	186.00	1.91	0.06	0.69
	Hurricane	0.800	0.043	186.00	18.78	**<0.001**	
	Cover:Fringe:Mangrove	0.003	0.002	186.00	2.11	**0.04**	
	Cover:Interior:Mangrove	−0.003	0.002	186.00	−1.94	**0.05**	
	Cover:Fringe:Marsh	0.004	0.002	186.00	0.17	0.86	
	Cover:Interior:Marsh	−0.006	0.002	186.00	−2.52	**0.01**	
Soil %S	Intercept	0.273	0.136	186.00	2.01	**0.05**	0.09
	Hurricane	0.266	0.070	186.00	3.78	**<0.001**	
	Cover:Fringe:Mangrove	−0.004	0.003	186.00	−1.52	0.13	
	Cover:Interior:Mangrove	−0.004	0.003	186.00	−1.41	0.16	
	Cover:Fringe:Marsh	−0.004	0.004	186.00	−1.22	0.23	
	Cover:Interior:Marsh	−0.007	0.004	186.00	−1.93	0.06	
Soil $\delta^{34}S$ (‰)	Intercept	−0.330	0.137	186.00	−2.40	**0.02**	0.07
	Hurricane	−0.003	0.071	186.00	−0.04	0.96	
	Cover:Fringe:Mangrove	0.009	0.003	186.00	3.26	**0.001**	
	Cover:Interior:Mangrove	0.007	0.003	186.00	2.59	**0.01**	
	Cover:Fringe:Marsh	0.001	0.004	186.00	0.40	0.69	
	Cover:Interior:Marsh	0.006	0.004	186.00	1.73	0.09	
Fine root biomass (g C/m^2)	Intercept	0.062	0.111	30.27	0.56	0.58	0.32
	Hurricane	0.506	0.073	6.01	6.98	**<0.001**	
	Cover:Fringe:Mangrove	0.005	0.002	190.57	2.04	**0.04**	
	Cover:Interior:Mangrove	0.012	0.002	190.57	5.09	**<0.001**	
	Cover:Fringe:Marsh	−0.008	0.003	190.64	−2.69	**<0.01**	
	Cover:Interior:Marsh	0.006	0.003	190.62	1.99	**0.05**	
Coarse root biomass (g C/m^2)	Intercept	0.418	0.141	129.00	2.95	**<0.01**	0.51
	Hurricane	0.837	0.077	129.00	10.85	**<0.001**	
	Cover:Fringe:Mangrove	0.003	0.002	129.00	1.02	0.31	
	Cover:Interior:Mangrove	0.002	0.002	129.00	1.09	0.28	
	Cover:Fringe:Marsh	0.001	0.004	129.00	0.38	0.70	
	Cover:Interior:Marsh	−0.005	0.004	129.00	−1.28	0.20	

Notes: Bolded values denote significance of $P < 0.05$ using $\alpha = 0.05$.

SE, standard error. Conditional R^2 was used to assess goodness of fit for linear mixed-effects models (includes variance of fixed effects and random effects; Nakagawa and Schielzeth 2013). A total of $n = 80$ soil cores were collected and analyzed. Data from pre-hurricane were collected in 2013 (see Charles et al. 2020). Data from post-hurricane were collected in 2017 and 2018. We report the mean value from post-hurricane years, except for $\delta^{34}S$ which changed from 2017 to 2018. Model results include significant ($\alpha = 0.05$) terms and overall model fit (conditional R^2 values and P values). When one vegetation type (marsh, mangrove) and/or cell location (fringe, interior) was significant, the category was specified in the table. Only vegetation type (marsh, mangrove) and/or cell location (fringe, interior) was specified in the table when both types were significant.

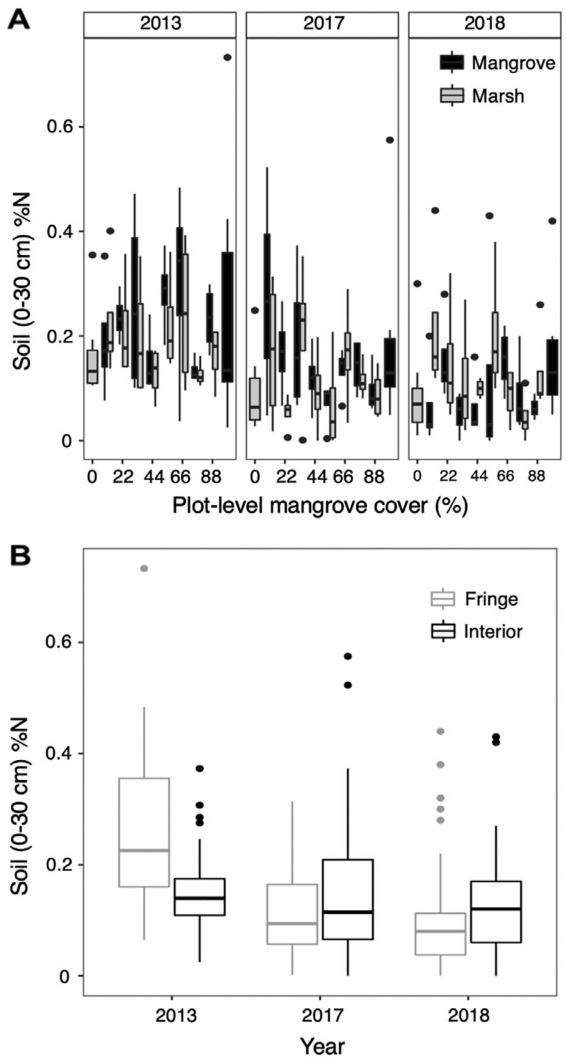

Fig. 3. Nitrogen (N) content (%) in soils (0–30 cm below marker horizons) from coastal wetland plots in Port Aransas, Texas, USA, from dates pre- (2013) and post-Hurricane Harvey (2017, 2018). Boxplots correspond to (A) wetland cells (3 × 3 m) of different vegetation type (marsh, gray; mangrove, black) along a gradient in plot-level percent mangrove cover and (B) fringe or interior locations of plots.

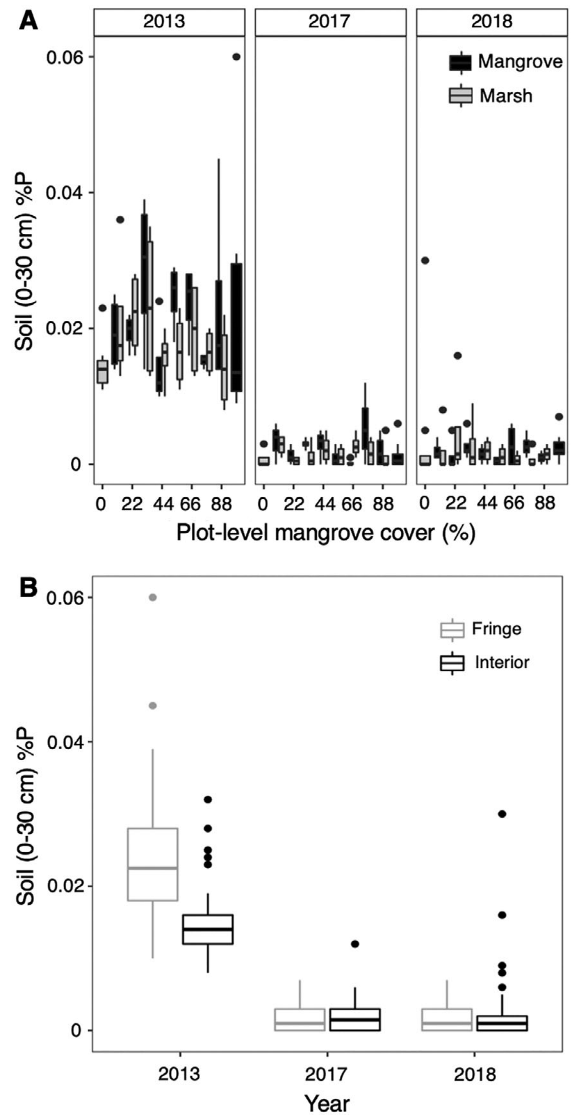

Fig. 4. Phosphorus (P) content (%) in soils (0–30 cm below the marker horizon) from coastal wetland plots in Port Aransas, Texas, USA, from dates pre- (2013) and post-Hurricane Harvey (2017, 2018). Boxplots correspond to (A) wetland cells (3 × 3 m) of different vegetation types (marsh, gray; mangrove, black) along a gradient in plot-level percent mangrove cover and (B) fringe or interior locations of plots.

than in marsh cells (Charles et al. 2020). We predicted that suspended marine sediments delivered by storm surge would supply a nutrient pulse (Nyman et al. 1995, Davis et al. 2004, Castañeda-Moya et al. 2010) in the accreted surface sediment that could increase root growth (McKee and Cherry 2009). Contrary to these hypotheses, chemical concentrations in surface accreted sediments decreased (%P) or were similar (%N, %S) from pre- to post-hurricane across vegetation treatments. Our findings diverge from previous studies in the Gulf of Mexico that have measured increased sediment P concentrations in marine

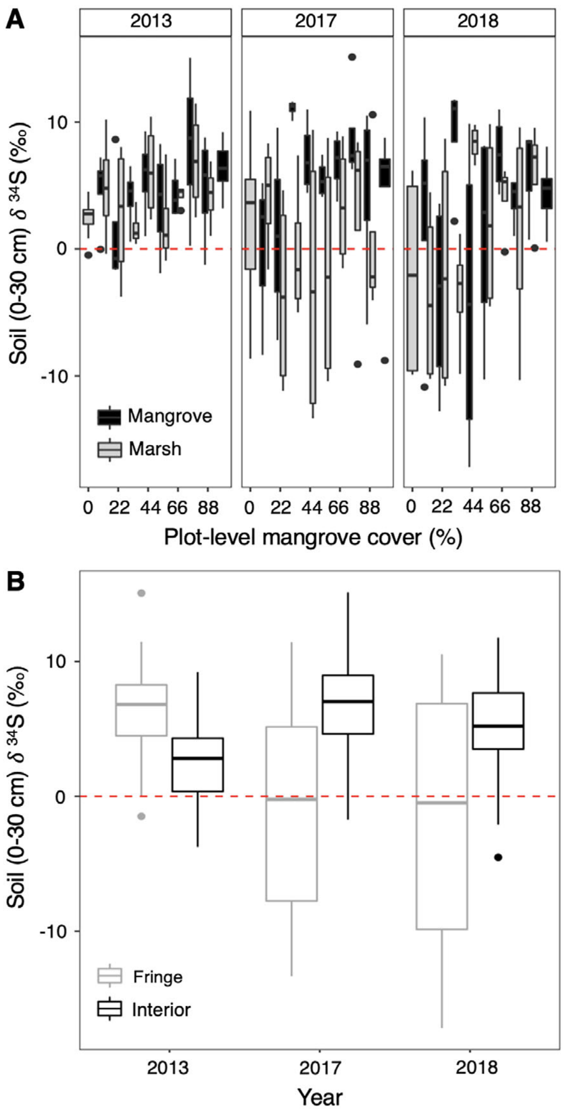

Fig. 5. $\delta^{34}S$ content (‰) in soils (0–30 cm below marker horizons) from coastal wetland plots in Port Aransas, Texas, USA, from dates pre- (2013) and post-Hurricane Harvey (2017, 2018). Boxplots correspond to (A) wetland cells (3 × 3 m) of different vegetation types (marsh, gray; mangrove, black) along a gradient in plot-level percent mangrove cover and (B) fringe or interior locations of plots.

sediment deposits from hurricane storm surge. For example, storm surge from Hurricane Wilma in the Florida Everglades increased sediment accretion in tidal riverine mangrove forests by 17× compared with annual vertical accretion rates, contributing to a net gain in surface elevation and sediment nutrient content (Castañeda-Moya et al. 2010, 2020). Prior to Hurricane Harvey, C and nutrients in accreted sediments were greater in mangrove than in marsh cells (Charles et al. 2020), but post-hurricane reductions in sediment nutrient concentrations and similarity between mangroves and marshes suggest that there was erosion of surficial sediment and soils followed by storm surge deposition of organic- and nutrient-poor sediments. In addition, the source and nutrient content of sediments determines whether sediments deposited by storms represent a subsidy or stress (Smith et al. 2009, Castañeda-Moya et al. 2010, Radabaugh et al. 2020). The reduction in %P and depletion in $\delta^{34}S$ in sediment and soil following Hurricane Harvey could partially explain reductions in root biomass in all wetlands. Our results indicate that storm surge sediments that are low in organic matter and nutrient content function more as a stress than a subsidy to hurricane-impacted wetlands through root burial and increased nutrient limitation.

Storm sedimentation is complex and drives heterogeneous responses in coastal vegetation. For example, sedimentation can interfere with gas exchange and nutrient cycling in wetland roots and soil (Lugo et al. 1981, Radabaugh et al. 2020), and delayed mangrove responses to hurricanes have been documented elsewhere along the Gulf Coast. After the passage of a Category 4 hurricane over the Florida Keys, mangrove island trees (*A. germinans* and others) suffered delayed mortality after nine months, which was attributed to root burial by storm surge deposits (Radabaugh et al. 2020). After the passage of Hurricane Wilma over the Florida Everglades, mangrove mortality, root loss, and soil substrate compaction were observed for up to three years despite leaf regrowth (Barr et al. 2012). Thus, although plants may recover aboveground from hurricanes, belowground burdens through reduced soil nutrients and root biomass can impact holistic recovery of coastal wetlands. However, long-term responses to hurricane-induced sedimentation have shown distinct periods of elevation loss followed by elevation gain driven by surface and subsurface processes (Feher et al. 2020). Further, the timing of storm surge can influence whether it is detected as a relative subsidy or stress. Recent evidence in marsh–mangrove ecotones, for example, illustrates the importance of wrack in facilitating mangrove

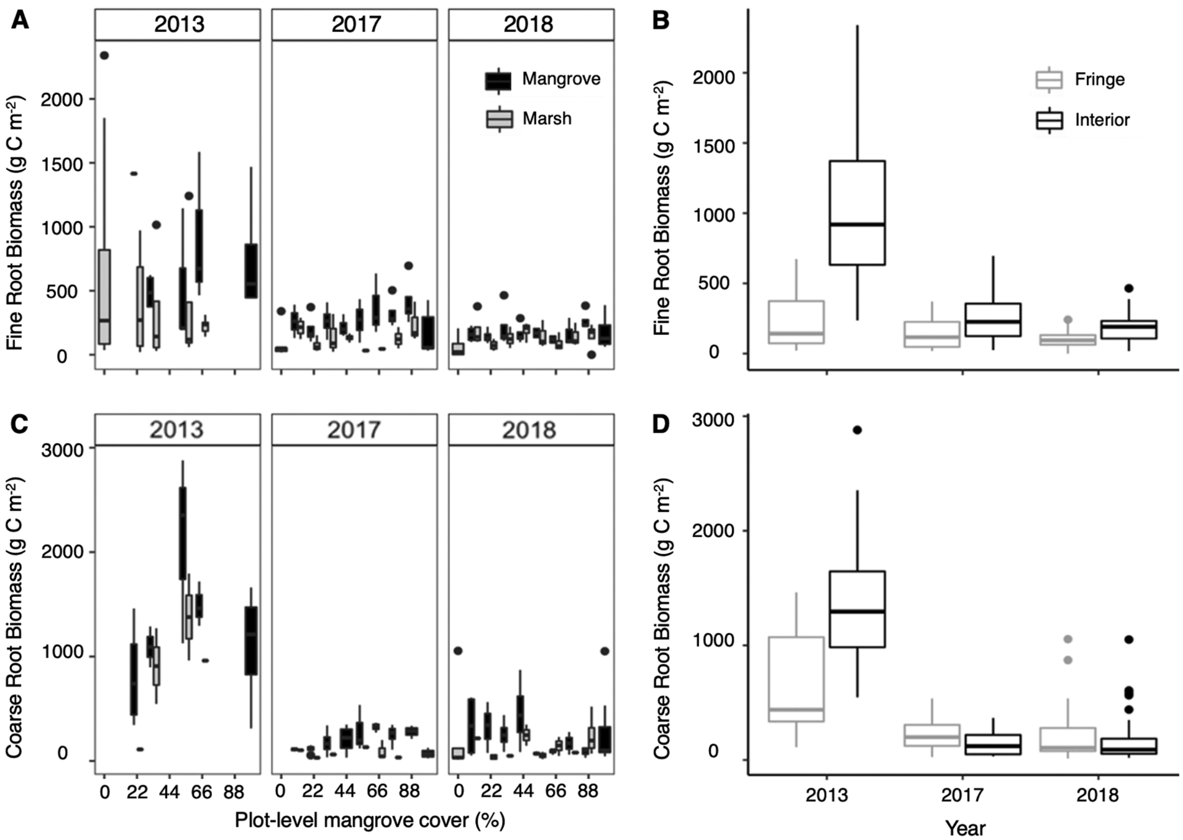

Fig. 6. Root biomass (g C/m^2; 0–30 cm below marker horizons) from coastal wetland plots in Port Aransas, Texas, USA, on dates pre- (2013) and post-Hurricane Harvey (2017, 2018). Boxplots correspond to (A, C) wetland cells (3 × 3 m) of different vegetation types (marsh, open; mangrove, filled) along a gradient in plot-level percent mangrove cover and (B, D) fringe or interior locations of plots.

propagule establishment into open marsh patches, which can be inhibited if storm surge pushes wrack out of critical and into marginal habitats (Smith et al. 2020).

A comprehensive understanding of above- and belowground recovery from hurricanes is needed in order to assess coastal wetland vulnerability to disturbances. According to a concurrent study quantifying damage by Hurricane Harvey to our experimental sites, black mangrove canopy cover in our plots decreased >20% from 2015 to 2017, presumably due to hurricane wind effects, with greatest defoliation observed in tall trees (>1.5 m) along the plot fringe (Armitage et al. 2020) that were not submerged by the storm surge and thereby protected from winds. Mangrove recovery was observed within weeks (Armitage et al. 2020), and reduction in root biomass stocks may partially reflect plant energy reallocation to regrowth aboveground following wind defoliation and cover damage (Radabaugh et al. 2020). However, defoliation was only common in the front of the plots, whereas root biomass loss occurred in both the fringe and interior of plots, indicating that reallocation of energy was not the only factor explaining decreases in root biomass. Rather, our findings suggest that nutrient limitation stress and sustained storm surge inundation may collectively cause root biomass loss in wetland plants lasting more than a year post-hurricane. Results from our study are most applicable to arid coastal wetlands of the Western Gulf of Mexico, where succulent marsh vegetation (e.g., *Batis*) dominates rather than *S. alterniflora* (Osland et al. 2016, Yando et al. 2016). Grasses such as *S. alterniflora* have very different structural morphologies compared with succulent plants such as *Batis*. Therefore, the effects of storm surge sedimentation, as well as enhanced nutrient limitation, following hurricanes may impact different marshes and marsh–mangrove ecotones differently (McKee et al. 2020). For example, unlike in our current study, *Spartina* marshes in Mississippi can capture more storm surge sediment than *A. germinans* mangroves (McKee et al. 2020). Globally, it is critical to better understand how plant identity and composition interact in areas of transitioning coastal ecosystems to influence responses to hurricanes.

Understanding the complex set of interactions among vegetation changes and episodic disturbances is critical for the long-term protection, management, and persistence of coastal ecosystems (Bracken et al. 2013, Duarte et al. 2015, Tully et al. 2019). Coastal ecosystem managers must understand and accommodate how disturbance legacies affect the ability to restore threatened and declining coastal ecosystems and their services in order to maintain shoreline protection services of coastal wetlands (Nicholls et al. 2007, Sheaves 2009, Rivera-Monroy et al. 2011, Dahl and Stedman 2013). Theoretical predictions of ecosystem maintenance through disturbance pulses (Junk et al. 1989, Odum et al. 1995, Polis et al. 1997, Yang et al. 2008, 2010) can be useful to help integrate subsidy-stress effects on net ecosystem functions (Odum et al. 1979, Wilson et al. 2019). Ecological theory can also help inform how ecosystem restoration and management are adaptively used to maintain ecosystem services in a world of global changes.

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Supporting Information

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